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POPULATION CHANGES IN BOREAL FOREST BIRDS IN SASKATCHEWAN AND MANITOBA

DAVID A. KIRK,[1] ANTONY W. DIAMOND,[2] ALAN R. SMITH,[3] GEORGE E. HOLLAND,[4] AND PAUL CHYTYK[5]

ABSTRACT.—We counted breeding birds at four plots in central Saskatchewan and four in western Manitoba in 1990–1992 to examine changes in species composition and abundance since the plots were originally surveyed in 1972–1973. In Saskatchewan, more species of Neotropical migrants decreased (16) than increased (9; $P > 0.05 < 0.1$). Combined densities of Neotropical migrants declined (14–44%) on all of the Saskatchewan plots; Tennessee Warblers (*Vermivora peregrina*), Red-eyed Vireos (*Vireo olivaceus*), and Ovenbirds (*Seiurus aurocapillus*) declined on the most plots and by the greatest magnitude and Black-throated Green Warblers (*Dendroica virens*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) also decreased. Six of seven Neotropical migrants showed the same direction of change as in a province-wide Breeding Bird Survey. Successional changes did not account for decreased densities of these five species, but they may partly explain increases in some other species. Fluctuations in food supply (e.g., spruce budworm [*Choristoneura fumiferana*]) could not explain changes, because some species that should have responded numerically to budworm outbreaks that occurred in the 1990s had increased whereas others had decreased at the same site. The surrounding forest remained continuous over the 17–18 years, so changes in forest area cannot account for the declines. In Manitoba, more Neotropical migrants increased (19) than decreased (11) according to combined densities from four plots. Combined densities of Neotropical migrants also increased at three of the four plots (33–123%). Ten of 15 Neotropical migrant species showed different 'trends' than a province-wide analysis of BBS data. All changes in Manitoba could be attributed to vegetation succession on the plots and forest fragmentation in surrounding landscapes. Trends in Saskatchewan may be representative of general declines within continuously forested boreal landscapes, whereas those in Manitoba may reflect reduced opportunities for breeding in

[1] *Aquila* Applied Ecologists, C.P. 47, Wakefield, Québec J0X 3G0 and % National Wildlife Research Centre, Canadian Wildlife Service, 100 Gamelin Blvd., Hull, Québec, Canada K1A 0H3.

[2] Atlantic Cooperative Wildlife Ecology Research Network, P.O. Box 45111, Univ. of New Brunswick, Fredericton, New Brunswick, Canada E3B 6E1.

[3] Environment Canada, Canadian Wildlife Service, Prairie and Northern Region, Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada S7N 0X4.

[4] 129 Burlington Way, Winnipeg, Manitoba, Canada R3Y 1C1.

[5] Apt. No. 7, 245 Ontario Street, Victoria, BC, Canada V8V 1N1.

continuous forest as the landscape is increasingly fragmented by agriculture. *Received 3 Nov. 1995, accepted 22 May 1996.*

Widespread declines have been reported among forest birds that breed in North America and spend the boreal winter in the tropics (Neotropical-Nearctic migrants', hereafter 'Neotropical migrants'). Much of the evidence for these declines comes from long-term breeding bird censuses and Breeding Bird Surveys (BBS) in fragmented and isolated forests of the eastern and central United States (Johnston and Hagan 1992; for reviews see Askins et al. 1990; Askins 1993; Peterjohn and Sauer 1994). Deforestation and land-use change in the landscape surrounding the sites, and vegetation successional change on the plots themselves, are the likely causes of most local declines (Askins et al. 1990). That songbird populations have not decreased in some continuously forested areas (e.g., Wilcove 1988) supports the hypothesis that the small size and isolation of many eastern forests are crucial factors in the decline of some Neotropical migrants. However, songbird declines in other continuous forests (e.g., Holmes and Sherry 1988) and other factors provide increasing evidence to suggest that populations of some Neotropical migrants are also affected by events in the tropical nonbreeding areas because of competition for limited, and ever-diminishing, habitat (Marra et al. 1993; Rappole and McDonald 1994; Petit et al. 1995; Sherry and Holmes 1995; 1996).

Possible causes of declines in Neotropical migrants proposed for eastern North America include factors in the breeding areas, during migration, and in the nonbreeding areas (e.g., Holmes et al. 1986; Robbins et al. 1989; Askins et al. 1990; Hussell et al. 1992; Rappole and McDonald 1994; Sherry and Holmes 1995; 1996). In the boreal mixed-wood forest region of western Canada, which has a high diversity of breeding species and is the centre of distribution for some Neotropical migrants (e.g. Connecticut Warbler—scientific names are in Appendices I and II; Diamond 1991), it remains uncertain whether comparable declines have taken place. Moreover, the relative importance of the factors that affect songbird populations in western Canada may differ from those in the eastern or other parts of the continent. Boreal forest has been less subject to intensive human settlement than areas farther south where permanent fragmentation has resulted. Consequently, increases in populations of ground predators and the brood-parasitic Brown-headed Cowbird that accompany forest fragmentation elsewhere and which have been implicated in the decline of songbird populations (Robinson et al. 1995a) may be less important. Furthermore, the landscape changes that occur predominantly involve forestry operations; cutover areas do not change in their land-use and, in-

deed, may superficially resemble natural disturbances such as forest fire even though their effects on the forest landscape may be quite different (Hunter 1993; Telfer 1993). Some boreal species that appear 'area-sensitive' near the edges of their range in the United States may be less so within the boreal forest biome because this is a naturally heterogeneous habitat (Welsh 1987a; e.g., Merriam and Villard 1991). Therefore, long-term studies in continuous forest may be helpful to isolate the effects of factors other than forest size, cowbird parasitism, and possibly predation on bird populations.

We attempt to assess whether or not Neotropical migrants have declined in part of the boreal forest of western Canada by comparing densities in the early 1990s on eight Breeding Bird Census (BBC) plots in two locations counted by A. J. Erskine in the early 1970s, and comparing these changes at each site with those indicated by Breeding Bird Survey (BBS) data over the entire province (although largely south of continuous boreal forest in Saskatchewan and, to a lesser extent, Manitoba). Neither data set is ideal: the BBS routes have been run erratically (Erskine 1993) and, like the BBS routes elsewhere, they sample forest-interior species poorly because they are roadside counts. Also the BBC plots were counted in only two years about 20 years apart. We recognize these inherent flaws in design, but we believe it is important to present the data because there are no other sources of information than can address the question. Similar comparisons (of plots counted far apart in time), by Ambuel and Temple (1982) in southern Wisconsin and Wilcove (1988) in the Great Smoky Mountains, have set important precedents for making maximum use of opportunities to repeat early censuses despite problems in their inherent lack of replication.

METHODS

Study areas.—We counted birds on two study sites each containing four plots ranging from 15 to 30 ha in area. All plots, while within the Mixedwood zone of the Boreal forest, differed to some degree in vegetation and so there are some problems with treating them as replicates. Those in Saskatchewan were in a continuously forested area near Doré Lake (Erskine 1973a–d). Michel Point (17.5 ha, 54°41′N, 107°15′W) is a mature mixed stand of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*) with a few balsam poplar (*Populus balsamifera*). Except for the north end, the understory is generally sparse. Mirasty Lake (17.6 ha, 54°28′N, 107°14′W) is an even-aged stand dominated by trembling aspen with small numbers of white spruce, balsam fir (*Abies balsamea*), and black spruce (*Picea mariana*). A dense shrub layer of balsam fir occurs in the northern 150 m, and at the southern end speckled alder (*Alnus rugosa*), balsam poplar, and black spruce saplings are more abundant. Appleby Bay (17.5 ha, 54°29′N, 107°16′W) is an uneven-aged stand dominated by balsam fir with white birch, white spruce, trembling aspen, and some balsam poplar. Young balsam fir forms a dense shrub layer, and there are many mature blowdowns. A younger stand, dominated by white birch, trembling

aspen, and white spruce occurs to the south. Doré Lake Airstrip (23.4 ha, 54°37′N, 107°23′W) is dominated by mature black spruce with little understory. Two small creeks within this site are bordered by willow (*Salix scouleriana*) and speckled alder.

The sites in western Manitoba, near Mafeking, were in a landscape increasingly influenced by agriculture but within the fringes of a large expanse of forest centred on the Porcupine Hills (Erskine 1972a–d). In 1972, Novra (17.5 ha, 52°31′N, 101°5′W) was a mature stand, undisturbed by human activity and dominated by balsam poplar and trembling aspen. The dense understory was composed mainly of mountain maple (*Acer spicatum*), beaked hazel (*Corylus cornuta*), and red osier (*Cornus stolonifera*). Speckled alder and willow (*Salix* spp.) occurred along three small brooks on the plot. By 1992, this stand had opened up considerably due to numerous blowdowns, creating more dense shrub in some locations and isolated large trees. The 1992 plot overlapped at least 95% with the 1972 plot; however, exact duplication of lines was not possible. Mafeking (17.5 ha, 52°47′N, 101°3′W) was a lowland black spruce stand; speckled alder and tamarack (*Larix laricina*) occurred in boggy gaps, and the main shrub was Labrador tea (*Ledum groenlandicum*). Around 1987, 30–40% of the 1972 plot was clear-cut, so in 1992 the plot was extended to the north in similar habitat to replace the cutover area. The northern 50% of the 1972 plot had changed little by 1992, except that trees were 1–2 m taller. Thus, this plot was 50% different and generally similar to that first surveyed in 1972, but lacking wet swales. Bellsite (29.25 ha, 52°35′N, 101°5′W) was dominated by jack pine (*Pinus banksiana*). Shrubs included Saskatoon serviceberry (*Amelanchier alnifolia*) and chokecherry (*Prunus virginiana*). Because the 1972 plot had been clear-cut and replanted with jack pine around 1987–1989 (30 cm height in 1992), an entirely new plot was established about 1.5 km farther north in roughly similar habitat but including small areas of planted pines. The Steeprock Bay plot (15.75 ha, 52°47′N, 100°55′W) was in a balsam fir and white birch stand with a few white spruces. The lower canopy was composed of white spruce and trembling aspen. According to Erskine (1972a–d), most large spruces were logged many years before. Where gaps occurred in the canopy, mountain maple, speckled alder (in wet areas), willow (*Salix discolor*), and beaked hazel grew. Changes since 1972 included clear-cutting of 10% of the 1972 plot and a further 10% cut-over for birch firewood. Thus, the 1992 plot was 10% smaller than the one censused in 1972. Also, windfalls of mature balsam fir had opened up the canopy.

Census techniques.—Territory mapping methods were used on all sites (Intl. Bird Census Comm. 1969; Bibby et al. 1992), and new 50-m grids for the 1990s censuses were placed as close as possible to the same lines used in the 1970s. In 1972 and 1973 all surveys were conducted by A. J. Erskine; PC censused the Saskatchewan plots in 1990 or 1991 and GEH censused the Manitoba plots in 1992. In Saskatchewan, plot coverage was from 27 May to 8 July in 1973 (8–10 visits per plot) and from 10 June to 28 June in 1990/1991 (9 visits per plot). Most counts in 1973 were between 04:05 and 12:46 h; in 1990 and 1991, most visits were between 04:13 and 11:40 h, with one evening visit (18:25–20:15 h). Less time was spent censusing each plot in 1973 because Erskine surveyed two plots each morning and all four plots (plus another wet-marshy bog census plot) in one year, whereas PC visited only one plot each morning and surveyed only two plots each year. The total counts from 1973 therefore are more likely underestimates compared with 1990–91. The weather in 1973 was generally cool with frequent rains (Erskine 1973a–d); in 1991 weather was similar, but in 1990 there was less cloud cover. In Manitoba, coverage was from 26 May to 7 July in 1972, and from 29 May to 24 June in 1992 (9 visits per plot for both periods). Counts were made between 04:55 and 13:22 h in 1972 and 04:30 to 12:45 h in 1992. Because GEH recorded more edge species and visitors, total counts for 1992 were higher than 1972 (A. J. Erskine pers. commun.). Erskine (1972a–d) recorded late May 1972 as being unusually

warm. Frosts occurred on several days in mid-June 1972 (15, 19, 20), but censuses were generally on warm days.

Vegetation sampling.—Vegetation was quantified using the 0.04-ha (0.1-acre) circle sampling method of James and Shugart (1970). Five (1990/1991) or 20–28 circles (1972/1973) were placed at 50-m intersections of the bird census plot (these were located systematically in 1972/1973, randomly in 1990/1991). Diameters of all trees > 3 cm diameter at breast height (dbh) were measured in each circle, and canopy height was estimated visually. Shrub density was calculated as in James and Shugart (1970). Both canopy and ground cover were recorded on the second of the two transects used to estimate shrub density. Slight differences in class diameters for shrubs and trees used by PC in 1990–1991 caused us to combine some categories to provide data equivalent (but not fully comparable) to those collected by Erskine in 1973. The same protocol was used for measuring vegetation at the Manitoba sites in 1972, but different methods used in 1992 allowed us to calculate only the relative abundance of different tree species.

Interpretation of territories.—Because the interpretation of field data on breeding territories can differ between people (Oelke 1981; Bibby et al. 1992), original field sheets from all plots in both surveys were re-interpreted by DAK. This procedure avoided the bias of using interpretations by different individuals; we could not control for differences between the three field observers (A. J. Erskine and PC, and A. J. Erskine and GEH). Although we did not use the published data analyses of Erskine (1972 a–d, 1973 a–d), we compared the number of territories for each species and found that, with few exceptions, they were quite similar. For this analysis, it was the relative differences in densities between periods that were important.

We based territory boundaries on simultaneous registrations (contemporary contacts) by two singing males, because this gave the best indication that two different individuals held adjacent territories (Intl. Bird Census Comm. 1969). Territories were also determined by locating distinct clusters of song contacts recorded on different occasions (Intl. Bird Census Comm. 1969). We considered both the number of censuses and the spread of dates over which the censuses were made to recognize a cluster of registrations as delineating a territory. We considered 10 days between the first and last survey to be adequate following Marchant (1983).

In general, we used Intl. Bird Census Comm. (1969) criteria for the minimum number of registrations necessary for denoting breeding pairs; we considered two registrations (irrespective of the number of censuses) adequate for Black-capped Chickadee, Boreal Chickadee, Brown Creeper, Red-breasted Nuthatch, and woodpeckers, as these (mostly resident) species probably started breeding prior to the first census. Likewise, two registrations were considered sufficient for evidence of breeding by Cedar Waxwings because their breeding season extended later than the census period. The minimum period criterion between first and last censuses was also waived for this species. Finally, we counted all clusters within the plot and estimated the proportional area occupied at the edges of the plot to calculate total number of territories. Where species did not hold any full territories (partial clusters), we used a trace value (0.1) to represent possible breeders and visitors. However, we did not include these records in the main breeding totals for guild analyses for each plot because of uncertainties about their status. However, we included probable breeders (those with a + status in Erskine 1972a–d, 1973a–d). We excluded the four waterbirds, diurnal raptors, and large corvids from analyses because these species range over large areas and are not censused accurately by spot-mapping on plots of the sizes used. Flyovers of White-winged Crossbills, Pine Siskins, and Evening Grosbeaks were included, in both the 1970s and 1990s and territories of social groups (some of these species may nest semi-colonially) delineated to roughly estimate numbers of breeding pairs.

Analysis of life history strategies.—We classified species according to migratory habit and examined changes in combined densities of Neotropical migrants, short-distance migrants, residents, and irruptive species to test the possibility that the pattern of change between the two census periods might differ by life history strategy. Migratory strategy was assigned based on the literature and Canadian Wildlife Service databases (D. A. Welsh and J. Pedlar, unpubl. data, C. Downes, pers. commun.). Neotropical migrants were species mainly spending the boreal winter in Central and South America (south of 30°N latitude), short-distance migrants wintered mainly within Canada or the United States (north of 20° N latitude), and resident species were present throughout the year. We also distinguished irruptive species (i.e., Evening Grosbeak, White-winged Crossbill, Pine Siskin, and Purple Finch). However, in statistical analyses we combined irruptive species with residents because of small sample sizes.

Breeding Bird Survey (BBS) analyses.—to determine whether the patterns we observed at local census plots were part of a regional population change, we examined results from the BBS from 1973–1991 for Saskatchewan and 1972–1992 for Manitoba (B. T. Collins, pers. comm.). Standard route-regression techniques were used for BBS analyses with modifications described in Downes and Collins (1996).

Statistical analyses.—We calculated the combined densities of each species for Saskatchewan and Manitoba plots separately for each census period (1970s or 1990s). We believe this is justified because there was no replication of each habitat type. Then, using these totals, we tested whether Neotropical migrants, short-distance migrants, or resident (or irruptive) species declined overall using a Wilcoxon's Matched Pairs test (Zar 1984); here we used the 0.1 values because of small sample sizes (we omitted species that were recorded only as visitors at the edge of plots). We used chi-square one-sample tests (after Wilcove 1988) to compare the combined numbers of Neotropical migrants, short-distance migrants, and resident/irruptive species between years. Yates' correction was used because there was only one degree of freedom in all cases (Zar 1984). Chi-square tests were performed on actual number of territories and not the corrected density estimates (presented in Appendices I and II for comparison among plots). Except where stated, all statistical tests are two-tailed. It may be inappropriate to apply statistical tests to our data because our samples were not randomly chosen from wider populations and our sample sizes are small. We emphasize that our study design was constrained by the establishment of the plots in 1972 and 1973 and that our purpose is to explain possible trends; we recognize the impossibility of proving definite trends from eight plots counted 20 years apart.

RESULTS

Avifaunal changes: Saskatchewan.—Of 25 Neotropical migrant species counted at the four sites, 16 decreased and nine increased (Appendix I). Based on the null hypothesis that overall densities of Neotropical migrants should increase with succession in western boreal forests (see Kirk et al. 1996), as in eastern North America (Mönkkönen and Helle 1989), this decrease approached statistical significance (T = 105.5, N = 25, one-tailed probability, $0.1 > P > 0.05$). However, there were marked decreases in five Neotropical migrant species; Red-eyed Vireos declined by 48% at Michel Point, where they were most abundant, and at two other sites (Mirasty Lake 65%, Appleby Bay 91%; Appendix I). At another site (Doré Lake) they occurred at low abundance in 1973 and disappeared

TABLE 1

CHANGES IN HABITAT VARIABLES IN SASKATCHEWAN AND MANITOBA CENSUS PLOTS

Site	Year	Ground cover (%)	Shrub density[a] (stems/ha)	Canopy cover (%)	Canopy height	
					$\bar{x}$	Range
Saskatchewan						
Michel Point	1973	82	1750	80	18.9	15.0–21.6
	1990	78	5625	74	23.5	20.5–26.4
Mirasty Lake	1973	63	2875 (5525)	71	10.2	6–12
	1991	76	6700	81	16.7	14.4–18.9
Appleby Bay	1973	54	2050 (4610)	72	16.2	9–24
	1991	57	6850	80	19.6	17.4–21.6
Doré Lake	1973	80	1738 (3350)	53	12.9	
	1990	90	6525	53	17.7	10.8–27.3
Manitoba						
Novra	1972	<50	23,000	75	17.1	9.0–21.0
	1992					
Mafeking	1972	98	2623	55	10.8	9.0–13.5
	1992					
Bellsite	1972	95	1255	42	8.1	6.0–12.0
	1992					
Steeprock Bay	1972	95	4143	64	12.6	9.0–16.5
	1992					

[a] Note that in 1972/1973 Erskine measured trees in 3.75–7.5 cm and >7.5 cm classes (in parenthesis), plus shrubs separately. PC measured shrubs <7.5 cm; thus Erskine's combined trees <7.5 cm and shrub classes should be equivalent to PC's estimates. However, other differences interfered with comparisons.

completely by 1990. Tennessee Warblers declined at all sites; by 98% at Michel Point, 69% at Mirasty Lake, 27% at Appleby Bay, and 39% at Doré Lake. Black-throated Green Warblers also declined at Michel Point (76%) and at Appleby Bay (67%). Ovenbirds declined (46%) at Michel Point and (29%) at Mirasty Lake. Rose-breasted Grosbeaks declined 92% at Michel Point and 83% at Appleby Bay (Appendix I).

In contrast to Neotropical migrants, there were no consistent patterns of declines across sites in 13 short-distance migrant species. Seven species declined, six increased, and in one there was no change ($T = 34.5$, N = 13, $P > 0.1$; Appendix I). However, there was a difference ($T = 3$, N = 11, $P < 0.02$) in the magnitude of the increases (9) and decreases (2) in irruptive and year-round resident species. This may be because of the widely fluctuating nature of local populations of nomadic species, depending on food supply.

Migratory status.—There were striking differences between the two count periods when we compared the overall number of individuals by migratory strategies (Fig. 1). The combined densities of Neotropical mi-

grants declined on all four plots (Fig. 1). Combined densities of Neotropical migrants declined 44% at Michel Point (χ^2 = 11.36, df 1, P < 0.001), 40% at Mirasty Lake (χ^2 = 3.52, df 1, P > 0.05) and 25% at Appleby Bay (χ^2 = 1.78, df 1, P > 0.1). The non-significant decrease (χ^2 = 0.17, df 1, P > 0.5) in numbers of Neotropical migrants at Doré Lake was much smaller (14%; Fig. 1). However, short-distance migrant species increased on all plots, although the densities were much lower; 184% at Michel Point (χ^2 = 1.76, df 1, P > 0.1), 135% at Mirasty Lake (χ^2 = 0.17, df 1, P > 0.5), and 37% at Doré Lake (χ^2 = 1.19, df 1, P > 0.1). There was little change in the combined densities of this group (10% increase) at Appleby Bay (χ^2 = 0, df 1, P > 0.9). Similarly, combined densities of resident and irruptive species increased at three sites, although the difference was significant only for Doré Lake (176%, χ^2 = 5.98, df 1, P < 0.025; Fig. 1). There was a slight decrease at Appleby Bay (5%).

Vegetation changes.—The vegetation at Michel Point had become slightly more uneven-aged over the period between censuses, with an increase in the proportion of larger trees (Fig. 2). Opening of the lower canopy may have occurred through windfall. There was an increase in relative density of white spruce, balsam fir (> 3 cm dbh), and aspen, but balsam poplar densities declined in 1991 (Fig. 3), possibly due to blowdowns. However, these differences could be attributed to sampling variation. Mirasty Lake was a successional aspen stand following a fire 30 years prior to the first census. This area had an increase in relative densities of white spruce and balsam fir (> 3 cm dbh; Fig. 3) and in canopy cover. Balsam fir dominated at Appleby Bay in both periods but there was a small increase in the proportion of aspen and a larger increase in white birch (Fig. 3). The increase in the proportion of shade-intolerant hardwood trees (Fig. 3) was accompanied by an increase in canopy cover (Table 1). The site that changed least in vegetation characteristics was Doré Lake Airstrip (Figs. 2, 3). However, there was a slight increase in relative density of black spruce, and more deciduous tree species were recorded in 1991 than 1973. The apparent increase in shrub densities at all sites (Table 1) may be unreliable because of differing sample sizes and methods; the relative values within years may, however, be useful.

Avifaunal changes: Manitoba.—There were no consistent patterns of declines or increases in Neotropical migrants over the 20-year period at the four sites in the Mafeking region (Appendix II). More species increased (19) than decreased (11), and the difference between years was not significantly different (T = 139, N = 30, P > 0.1). Of the species that decreased, the Solitary Vireo was most notable (by 89% at Steeprock Bay, 86% at Bellsite and 18% at Mafeking). Other species such as Tennessee Warbler disappeared at Bellsite and Mafeking but stayed the same

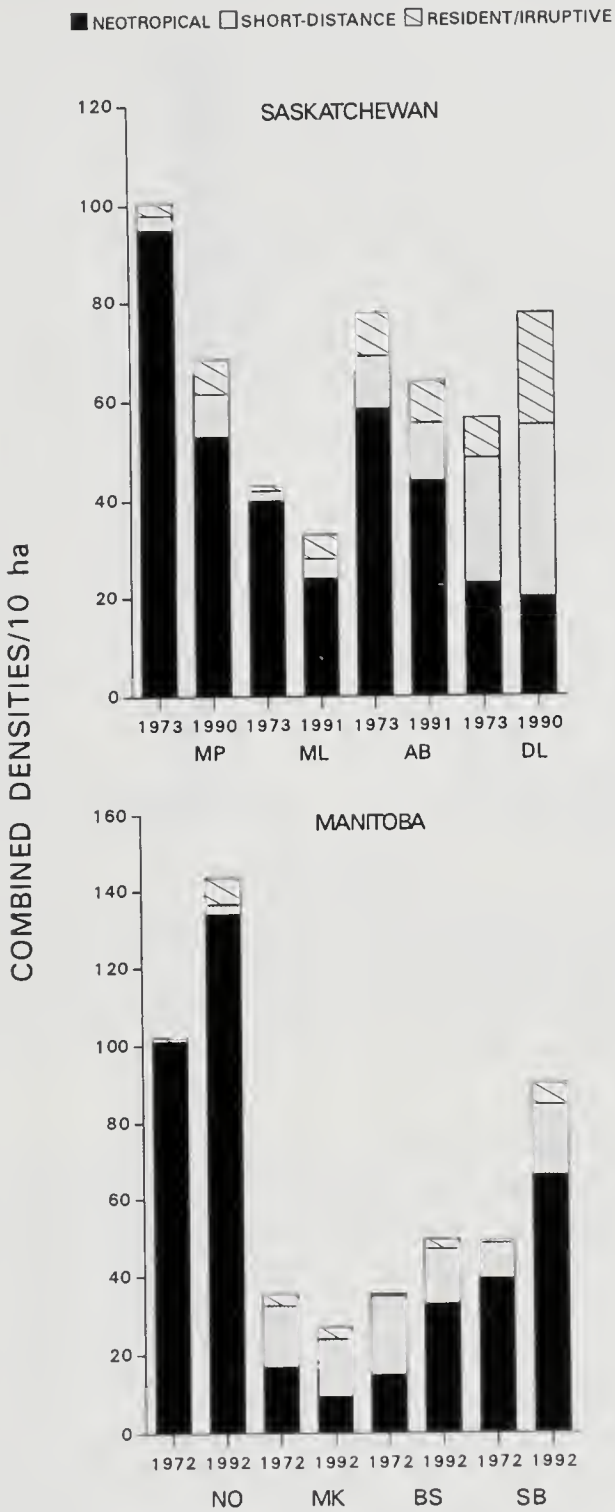


FIG. 1. Combined densities of Neotropical migrants, short-distance migrants, and residents/irruptive species. MP = Michel Point, ML = Mirasty Lake, AB = Appleby Bay, DL = Doré Lake; NO = Novra, MK = Mafeking, BS = Bellsite, SB = Steeprock Bay.

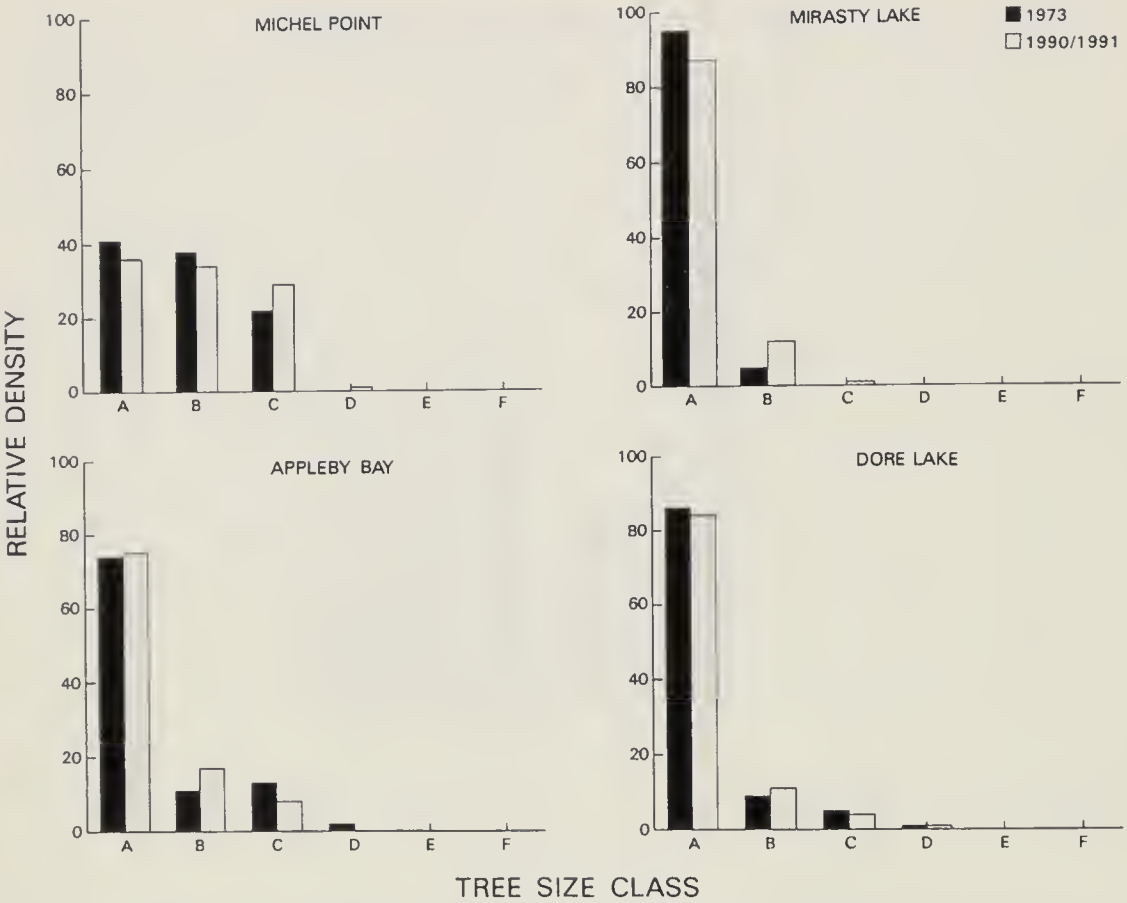


FIG. 2. Changes in proportions of tree size classes at Michel Point, Mirasty Lake, Appleby Bay, and Doré Lake Airstrip (size classes: A = 7.5–15 cm, B = 17.5–22.5, C = 32.5–37.5, D = 40.0–52.5, E = 55.0–67.5, F = 70.0–82.5). Erskine (1973) also considered trees of 3.5–7.5 cm diameter but these are excluded from analysis here.

(at Novra) or increased (at Steeprock Bay). Both of these species occurred at relatively low densities. The magnitude of change in the species that increased was far greater: at Novra, Least Flycatcher increased (200%) as did Swainson's Thrushes (248%), Red-eyed Vireos (100%) and Canada Warblers (406%). At Steeprock Bay, increases were found for Magnolia Warbler (32%) and Ovenbird (340%). Of the short-distance migrants, eight increased and nine decreased ($T = 54.5$, N = 17, $P > 0.1$; Appendix I). There was a significant increase in abundance of residents and irruptive species ($T = 16.5$, N = 15, $P < 0.02$), with 12 increasing and only three decreasing.

Migratory status.—Combined densities of Neotropical migrants increased significantly at three plots in Manitoba; 33% at Novra ($\chi^2 = 4.36$, df 1, $P < 0.05$), 67% at Steeprock Bay ($\chi^2 = 6.16$, df 1, $P < 0.025$), and 125% at Bellsite ($\chi^2 = 6.02$, df 1, $P < 0.025$; Fig. 1). The only site where this group declined (41%) was at Mafeking ($\chi^2 = 1.59$, df 1, $P > 0.1$).

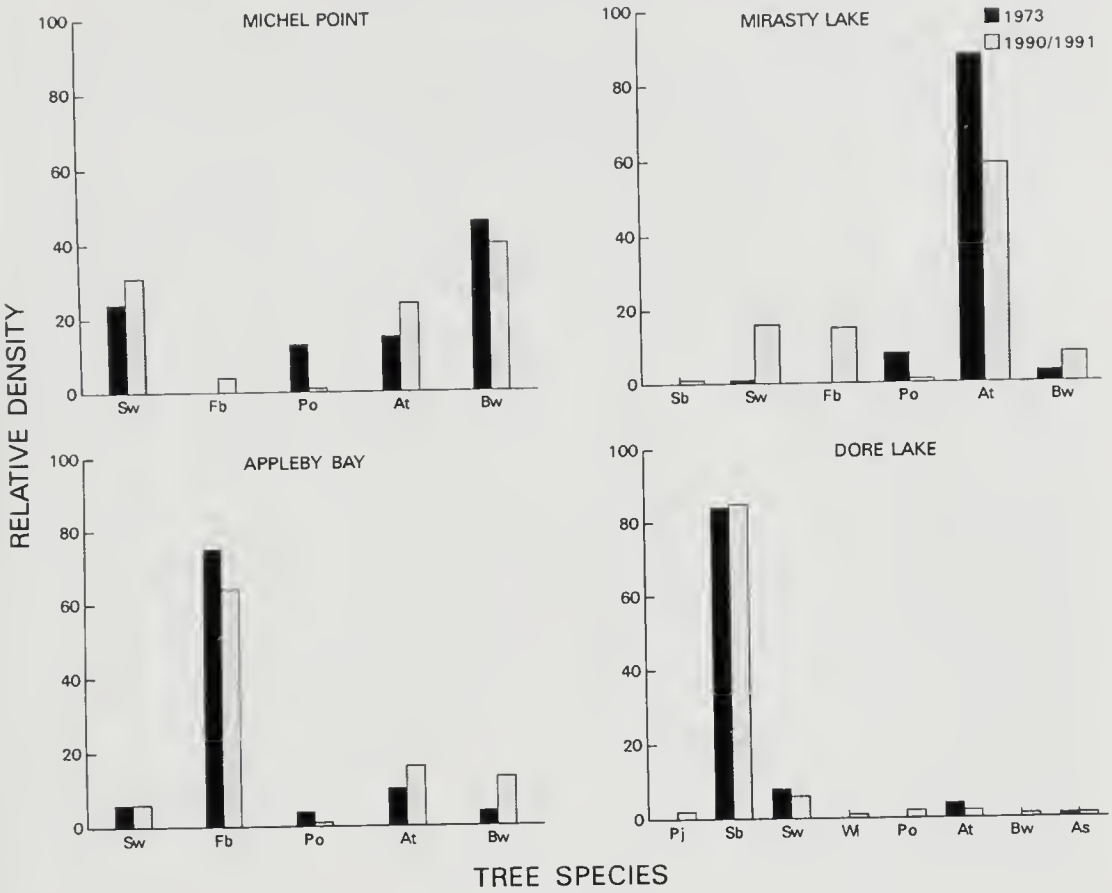


FIG. 3. Changes in proportions of tree species at Michel Point, Mirasty Lake, Appleby Bay, and Doré Lake Airstrip (tree species: Pj = jack pine, Sb = black spruce, Sw = white spruce, Fb = balsam fir, Wi = scouler willow, Po = balsam poplar, At = trembling aspen, Bw = white birch, As = speckled alder)

Short-distance migrants increased non-significantly at Steeprock Bay (106%, $\chi^2 = 2.63$, df 1, $P > 0.1$); low densities at Novra prohibited statistical testing. There were non-significant decreases in this group at Mafeking and Bellsite ($\chi^2 = 0$, df 1, $P > 0.9$ and $\chi^2 = 0.74$, df 1, $P > 0.5$, respectively). Resident and irruptive species increased at all sites, but none of the increases were significant and actual densities were very low (Fig. 1).

Vegetation changes.—The plot that differed most in its vegetation structure over the 20-year period was Novra. This balsam poplar site was mature at the time of the first census. By 1992, this stand had become open because of aging and windthrow; hence the decline in relative densities of poplar, aspen, and birch (Fig. 4). Consequently, there were more open areas and probably increased shrub density at this site, as well as isolation of mature trees. At Steeprock Bay, increased shrub densities were a result of a more open canopy cover due to logging and windthrow.

TABLE 2

BREEDING BIRD SURVEY RESULTS FOR SASKATCHEWAN AND MANITOBA (B. T. COLLINS, PERS. COMMUN.)

	Saskatchewan 1973–1991				Manitoba 1972–1992			
			Mean abundance				Mean abundance	
Species	% change	N	73	90/91	% change	N	72	92
Long-distance migrants								
Least Flycatcher	3.4**[a]	42	2.6	4.6	−3.2	34	8.8	4.6
Great Crested Flycatcher	—	—	—	—	1.6	26	0.8	1.0
Veery	—	—	—	—	1.9	24	0.6	0.9
Swainson's Thrush	−5.8	11	2.7	0.9	−2.2	15	3.8	2.4
Red-eyed Vireo	0.4	33	3.6	3.9	−0.7	32	6.8	5.9
Tennessee Warbler	−3.0	12	1.2	0.7	1.1	20	1.1	1.4
Nashville Warbler	—	—	—	—	−7.0	14	8.8	2.1
Yellow Warbler	1.5**	43	4.1	5.4	—	—	—	—
Chestnut-sided Warbler	—	—	—	—	2.5	15	1.5	2.4
American Redstart	—	—	—	—	−7.4	18	0.6	1.2
Ovenbird	−7.6	13	3.6	0.9	2.2	18	3.1	4.7
Connecticut Warbler	—	—	—	—	−7.6	15	2.5	0.5
Mourning Warbler	—	—	—	—	−2.2	19	3.6	2.3
Common Yellowthroat	—	—	—	—	−2.4	33	7.6	4.6
Rose-breasted Grosbeak	−0.1	18	0.9	0.9	−4.9	29	2.1	0.9
Clay-colored Sparrow	—	—	—	—	−2.9	33	21.2	11.7
Short-distance migrants								
Ruby-crowned Kinglet	—	—	—	—	0.9	13	1.5	1.7
Hermit Thrush	6.5**	12	0.6	1.9	1.1	14	2.1	2.6
Cedar Waxwing	—	—	—	—	−6.5	30	5.9	1.5
Yellow-rumped Warbler	—	—	—	—	5.1	17	0.9	2.5
Chipping Sparrow	−10.6	37	4.6	0.6	−0.9	34	4.3	3.6
Vesper Sparrow	—	—	—	—	0.9	30	5.9	7.0
Song Sparrow	—	—	—	—	−1.8	34	13.9	9.7
White-throated Sparrow	2.3	13	2.1	3.1	−1.6	19	7.4	5.4
Dark-eyed Junco	−1.5	10	0.8	0.6	—	—	—	—
Irruptive species								
Pine Siskin	1.0	13	0.5	0.6	—	—	—	—
Purple Finch	—	—	—	—	6.2	14	4.7	0.2
Year-round residents								
Ruffed Grouse	−1.6	17	0.5	0.4	—	—	—	—
Downy Woodpecker	—	—	—	—	1.5	26	0.4	0.5
Hairy Woodpecker	—	—	—	—	−0.9	29	0.7	0.6
Pileated Woodpecker	—	—	—	—	4.1	16	0.3	0.7
Gray Jay	—	—	—	—	−0.9	11	2.3	2.0
Black-capped Chickadee	−0.5	25	0.8	0.7	—	—	—	—
White-breasted Nuthatch	—	—	—	—	−14.8	15	0.2	0.7

[a] Significance levels are * $0.05 < P < 0.1$; ** $P < 0.05$). Species with abundance values of ≤ 0.2/10 ba for 1970s or 1990s in Appendices I and II are excluded.

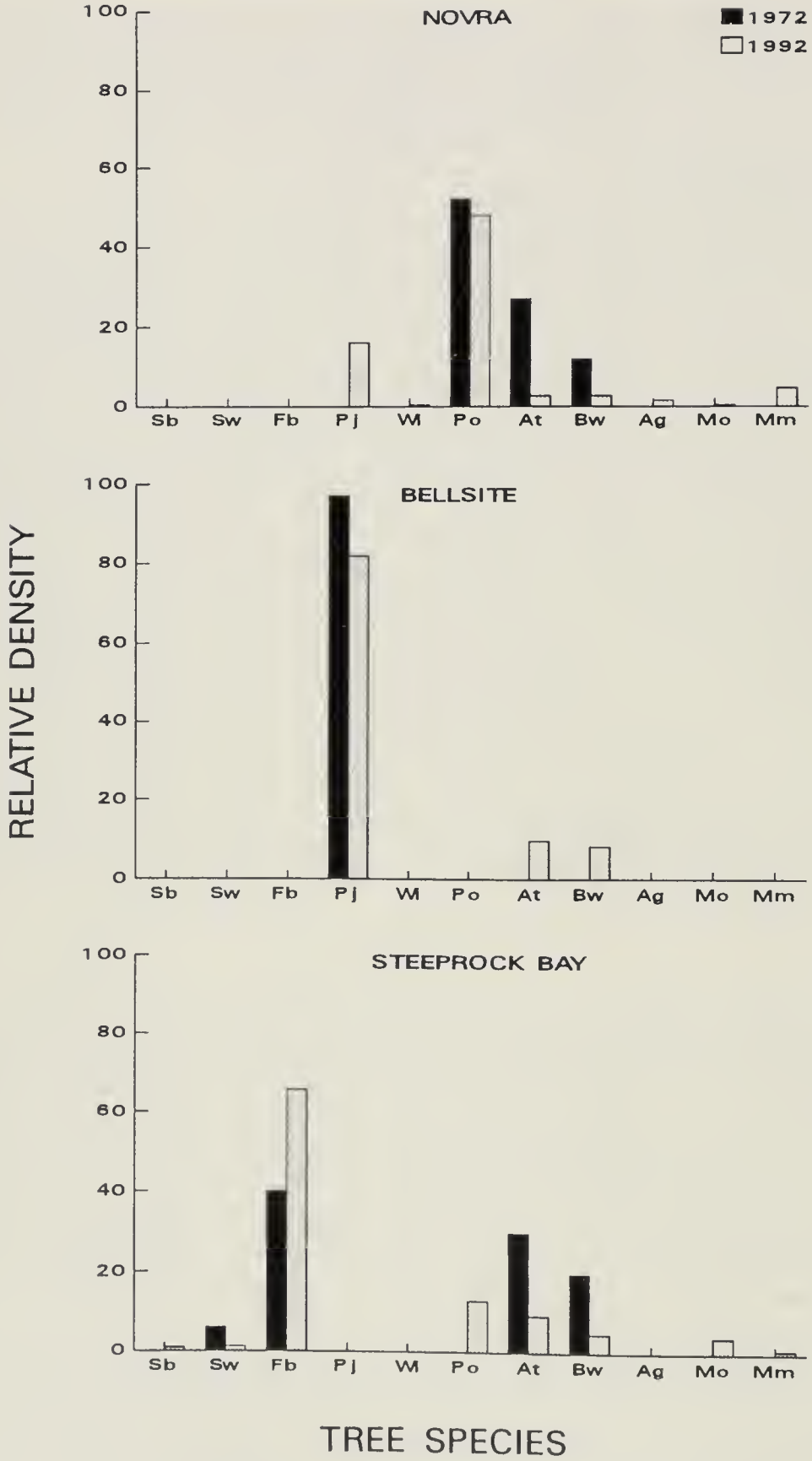
It is not surprising that few vegetation changes occurred at the Mafeking site because it was dominated by black spruce and succession in such stands is slow. At Bellsite, the jack pine plot was more mixed than that surveyed in 1972; the deciduous component was greater (Fig. 4) and pines were of larger size.

Breeding Bird Survey results.—We compared our data with analyses from the Breeding Bird Survey for the periods 1973–91 and 1972–92 for each province, respectively, to see if similar trends were reported at the scale of entire provinces (B. T. Collins, pers. commun.). The same direction of regression coefficients was found in the BBS as in the changes at our study sites in Saskatchewan for six of the seven Neotropical migrants reported on 10 or more routes (compare Appendices I and II vs Table 2). For example, there was a significant increase in Least Flycatchers and Yellow Warblers according to the BBS. Most strikingly, two of the species that showed the greatest declines in our study (Tennessee Warbler and Ovenbird) had negative regression coefficients according to the BBS for Saskatchewan (Table 2). However, Red-eyed Vireos had a positive regression coefficient (Table 2). In contrast to the results for Saskatchewan, the direction of BBS regression coefficients for Neotropical migrants in Manitoba were often opposite to the results we found (10 out of 15 cases; Table 2). For example, while Least Flycatchers decreased significantly in Manitoba over the long-term, they increased at one of our sites and began breeding at two others. However, unless the slope in route-regression analyses are significant, the direction of BBS regression coefficients may not be meaningful, so we urge caution in the interpretation of these comparisons.

DISCUSSION

We acknowledge the limitations of our data, which compare only two points in time two decades apart; we recognize that populations may have fluctuated considerably in the intervening years (e.g., Holmes and Sherry 1988; Blake et al. 1994). We do not know how representative our plots may be of boreal mixed-wood forests in the region in general, and we acknowledge that changes apparent on small plots may be stabilized at larger geographic scales (the metapopulation level; Villard et al. 1992). Nevertheless, our data are the first long-term plot-based 'trends' to be reported from an important area of the boreal forest, and they illustrate some problems of more general interest.

Although Neotropical migrants as a group did not decline significantly in Saskatchewan, five species declined on all plots where they were censused over the 17-year period, and combined densities of Neotropical migrants decreased on all sites. In contrast, Neotropical migrant numbers


NOVRA
1972
1992
BELLSITE
STEEPROCK BAY
RELATIVE DENSITY
TREE SPECIES
0
20
40
60
80
100
Sb
Sw
Fb
Pj
Wl
Po
At
Bw
Ag
Mo
Mm

tended to increase or remain stable in Manitoba. The Saskatchewan results recall those from fragmented forests in the eastern U.S., rather than those reported by Wilcove (1988) in the extensive forests of the Great Smoky Mountains; yet our Saskatchewan plots were in contiguous, unfragmented forest. The changes in bird abundance in Saskatchewan also run counter to predictions that Neotropical migrant numbers should increase as the forest matures (Mönkonen and Helle 1989) as found at other sites in western Canada (Kirk et al. 1996).

Regional differences in population trends of Neotropical migrants have been described elsewhere (James et al. 1992; Sauer and Droege 1992). We believe that the differences we found between the provinces are partly attributable to forest succession and the more fragmented nature of the landscape of the Manitoba plots. These were already somewhat fragmented by human settlement in 1972, and much forest has since been cleared for agriculture, mainly on the Swan Lake plain but also by the highway close to Mafeking. Logging has also become more widespread since a pulp mill was opened at La Pas in the mid 1980s, and a new mill is about to open in the Mafeking area (P. Rakowski, pers. commun.). The Manitoba plots, although still in forest, are now adjacent to an increasingly agricultural landscape; the Saskatchewan plots, in contrast, remain in a predominantly unfragmented forested landscape. The Manitoba study area is close to continuous forest in the Porcupine Hills which has high populations of Neotropical migrants (A. R. Smith pers. obs.). Thus, this census area may function as a population sink (sensu Pulliam and Danielson 1991; Villard et al. 1992). High apparent densities of Neotropical migrants have been found in fragmented boreal forest elsewhere in Saskatchewan (K.A. Hobson, pers. commun.) and in isolated, fragmented forests in the United States (Robinson et al. 1995a; Brawn and Robinson 1996).

In a comparison of bird populations trends between 1969–1986 at local (Hubbard Brook Experimental Station, New Hampshire) and regional scales (BBS statewide trends), Holmes and Sherry (1988) found that 10 of 19 bird species followed the same direction of trends. More species showed significant declines than increases at both the local (8 vs 1) and regional scale (5 vs 1). However, only three Neotropical migrant species decreased significantly at both scales (Least Flycatcher, Swainson's

←

FIG. 4. Relative densities of different tree species at (a) Novra, (b) Bellsite and (c) Steeprock Bay (Sb = black spruce, Sw = white spruce, Fb = Balsam fir, Pj = jack pine, Wi = willow species, Po = balsam poplar, At = trembling aspen, Bw = white birch, Ag = speckled alder, Mo = mountain maple, Mm = Manitoba maple).

Thrush, and Wood Thrush). Our analysis of BBS results over the same periods as encompassed by our study supports our finding that Tennessee Warblers and Ovenbirds may have declined in Saskatchewan boreal forest. Banding data since the 1950s also suggest that Tennessee Warblers may be declining in Saskatchewan (Smith and Diamond 1993), although trends in this species are difficult to determine because it is a budworm specialist. These results suggest that the declines we observed in Saskatchewan may not be limited to our plots but may be part of larger-scale phenomena. The BBS data are not conclusive either, because the regression coefficients were not statistically significant and may reflect cyclic population fluctuations (Hussell et al. 1992); densities of Tennessee Warblers fluctuated dramatically (Welsh 1987b) and were 'puzzlingly high' on the Saskatchewan plots in 1973 (A. J. Erskine, pers. commun.). Ovenbird populations may also fluctuate greatly from year to year in fragmented habitats (Gibbs and Faaborg 1990).

Because the Saskatchewan sites were not logged or the surrounding forest fragmented in the 17 years between counts, what might have caused the declines in the five species of Neotropical migrants? In a 16-year study of bird populations on a 10 ha plot at the Hubbard Brook Experimental Station, New Hampshire, Holmes et al. (1986) identified five factors that affected songbird population densities; (1) food supply (especially defoliating Lepidoptera); (2) poor spring weather conditions; (3) forest successional changes; (4) competitive interactions and (5) nonbreeding mortality. We will address each of these in turn.

At Hubbard Brook, Lepidopteran outbreaks accounted for high densities of Scarlet Tanager (*Piranga olivacea*), Least Flycatcher, Red-eyed and Philadelphia vireos and most warbler species during the first three years of study; long-term declines were attributed to lows in Lepidopteran populations which fluctuate on a 6–10 year irregular basis (Holmes et al. 1986). Evidence for changes in food supply causing bird density changes in our study area was weak; unfortunately, we had little information on the timing of Lepidopteran outbreaks. Although spruce budworm (*Choristoneura fumiferana*) outbreaks struck Mirasty Lake and Appleby Bay in 1990 and 1991, among budworm specialists only Bay-breasted Warblers showed numerical increases, while Cape May Warblers were new breeders at Appleby bay in 1991. Contrary to expectations, Tennessee Warblers declined dramatically at both sites; declines in other warbler species that should also respond numerically to budworm irruptions (Hussell et al. 1992) argue against the food supply hypothesis for the Saskatchewan sites. So far as we know the only other Lepidopteran outbreak was of tent caterpillars (*Malacosoma disstria*) which defoliated aspens near Michel Point in 1973. Subsequent movement by Red-eyed Vireos

seeking alternative foraging habitat in the birch on that plot could explain the high densities in 1973.

Cold, wet weather in late May (1974) was linked to declines in Scarlet Tanagers and several other species at Hubbard Brook (Holmes et al. 1986). While rain occurred on most survey days in 1973 in this study (A. J. Erskine, pers. commun.), the weather was dry in 1990 or 1991. Had weather influenced counts, bird numbers should have increased between censuses, not decreased.

Changes in habitat suitability possibly accounted for the decline of Least Flycatchers, Philadelphia Vireos, and Wood Thrushes at Hubbard Brook (Holmes et al. 1986). Our 1990s vegetation surveys were not strictly comparable with those of 1973; they do not show the requisite changes in forest structure that could have caused declines in the five species in Saskatchewan, but the differences in bird numbers recorded in Manitoba were consistent with succession.

Interspecific aggression by Least Flycatchers affected habitat use by American Redstarts at Hubbard Brook. We have no data on interspecific competition, but the bird communities were similar in the two study areas, so this factor is unlikely to have been important.

Finally, evidence for winter limitation on breeding numbers at Hubbard Brook was found for Dark-eyed Junco and Hermit Thrush, both of which declined after cold winters in the United States; little evidence was found to suggest that Neotropical migrants were affected by events during the nonbreeding season. While the effect of tropical habitat change is controversial (Hutto 1988, Robbins et al. 1989, Askins et al. 1990, Hussell et al. 1992), it is now recognized that nonbreeding survival rates for many species depend on the availability of suitable forest habitat in the Neotropics, which is declining rapidly.

Except for the Red-eyed Vireo, which spends the boreal winter in South America, there is considerable overlap in the nonbreeding distribution of Tennessee Warbler, Black-throated Green Warbler, Ovenbird, and Rose-breasted Grosbeak (Rappole et al. 1995), all species that declined at the Saskatchewan plots. The main difference is that Tennessee Warblers do not 'winter' in the Caribbean, while Black-throated Green Warblers and Ovenbirds do. Also the range of Rose-breasted Grosbeaks extends farther into South America than those of the warblers, occurring in much of Venezuela and Colombia, as well as Ecuador and Peru (Rappole et al. 1995). Most nonbreeding habitat for Red-eyed Vireos is in the Amazon Basin (Brazil), while for Tennessee Warblers, Black-throated Green Warblers, and Ovenbirds it is in western or southern Mexico. Most nonbreeding habitat for Rose-breasted Grosbeaks is in Colombia and Panama and, to a lesser extent, Mexico (Diamond 1986). Thus, the possibility exists

that where the nonbreeding areas of some Saskatchewan subpopulations of these species overlap, they are all being affected by loss of preferred habitat. Both Black-throated Green Warbler and Ovenbird were included by Petit et al. (1995) in a list of 45 species vulnerable to destruction of tropical broadleaved forests.

Recent studies suggest that the species that declined at the Saskatchewan plots use a range of forest habitats in the Neotropics (Hutto 1992; Greenberg 1992; Wunderle and Waide 1993; see review by Petit et al. 1995). In the Caribbean, Yucatan Peninsula, and western Mexico, Black-throated Green Warblers and Ovenbirds occur at highest densities in forest (Hutto 1992; Greenberg 1992; Wunderle and Waide 1993) and are considered forest generalists (Lynch 1989; Greenberg et al. 1995). Red-eyed Vireos are most abundant in early to mid-successional or edge habitats and are relatively rare in primary forests in the Amazon lowlands and adjacent Andes (S. K. Robinson, pers. commun.; Robinson et al. 1995b). Tennessee Warblers prefer patches of remnant forest and open woodland (e.g. Costa Rica; Powell et al. 1992), and Rose-breasted Grosbeaks use field-forest vegetation in western Mexico and the Yucatan (Lynch 1989; Hutto 1992). However, evaluating habitat for Neotropical migrants based on the distinction between forest and non-forest habitats may be a false dichotomy. While none of the above species uses completely open agricultural field habitats, they do use forest patches, gallery strips, or hedgerows within human-altered landscapes. As has been pointed out by others (Lynch 1989; Greenberg 1992; Petit et al. 1995), decreased habitat suitability may not just involve loss of mature forest; in much of the Neotropics second growth and forest habitat patches are also disappearing rapidly. Also, habitat use of Neotropical migrants is usually assessed from point counts or mist-net surveys in small areas, without measures of survival or differing social systems. That more individuals of Neotropical migrants are counted in early successional or patchy habitats, therefore, does not contradict the hypothesis that populations could be partly limited during the boreal winter (see Rappole and McDonald 1994). For example, Tennessee Warblers occur at highest densities in coffee plantations in parts of Mexico (Greenberg et al. 1995; in press). The shift from shade coffee to sun coffee in recent years in parts of the Neotropics may have become a limiting factor for this species because of loss of flowering tree species important for foraging (R. Greenberg pers. commun.).

However, since the same species that declined in Saskatchewan did not do so in Manitoba, and considerable mixing of populations is likely in the Neotropics (Wilcove and Terborgh 1984), it seems hard to attribute the trends we found to effects in the nonbreeding areas. It is possible, however, that the Manitoba densities were raised by successional and

fragmentation influences sufficiently to mask or reverse an underlying downward trend reflected in the contiguous forests of Saskatchewan.

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Appendix I

Estimated Number of Pairs/10 ha at Doré Lake, Saskatchewan Census Sites

Common and scientific name	Michel Point		Mirasty Lake		Appleby Bay		Doré Lake		Total	
	1973	1990	1973	1991	1973	1991	1973	1990	1973	1990–91
Long-distance migrants										
Olive-sided Flycatcher (*Contopus borealis*)							0.1		0.1	0
Yellow-bellied Flycatcher (*Empidonax flaviventris*)			0.1	0.9	0.1			0.1	0.2	1.0
Alder Flycatcher (*E. alnorum*)							0.1		0.1	—
Least Flycatcher (*E. minimus*)	4.6	6.9							4.6	6.9
Swainson's Thrush (*Catharus ustulatus*)		0.6	1.7	2.3	6.3	4.0	0.9	0.9	8.9	7.8
Solitary Vireo (*Vireo solitarius*)						1.7		0.9	0	2.6
Philadelphia Vireo (*V. philadelphicus*)			0.6	0.1					0.6	0.1
Red-eyed Vireo (*V. olivaceus*)	15.4	8.0	3.1	1.1	1.1	0.1	0.1		19.7	9.2
Tennessee Warbler (*Vermivora peregrina*)	8.0	0.2	7.4	2.3	6.3	4.6	5.6	3.4	27.3	10.5
Yellow Warbler (*Dendroica petechia*)		1.7							0	1.7
Magnolia Warbler (*D. magnolia*)		1.1	0.3		5.7	0.1		0.1	6.0	1.3
Cape May Warbler (*D. tigrina*)						1.1	1.7	0.9	1.7	2.0
Black-throated Green Warbler (*D. virens*)	4.6	1.1			4.3	1.4			8.9	2.5
Blackburnian Warbler (*D. fusca*)	0.1	0.2							0.1	0.2
Palm Warbler (*D. palmarum*)				0.1					0	0.1
Bay-breasted Warbler (*D. castanea*)	2.3	0.1		0.9	6.3	9.1	0.4	0.4	9.0	10.5
Black-and-white Warbler (*Mniotilta varia*)			1.1	0.1					1.1	0.1
American Redstart (*Setophaga ruticilla*)			0.1						0.1	0
Ovenbird (*Seiurus aurocapillus*)	16.0	8.6	8.0	5.7		0.1+			24.0	14.4
Mourning Warbler (*Oporornis philadelphia*)	0.1								0.1	0
Canada Warbler (*Wilsonia canadensis*)			0.1		0.3				0.4	0
Western Tanager (*Piranga ludoviciana*)		1.1							0	1.1
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1.2	0.1			0.6	0.1			1.8	0.2
Chipping Sparrow (*Spizella passerina*)	2.3	0.6	0.6	0.6	2.3	2.9	1.5	1.7	6.7	5.8
Lincoln's Sparrow (*Melospiza lincolnii*)							0.1		0.1	0
Short-distance migrants										
Yellow-bellied Sapsucker (*Sphyrapicus varius*)					0.1				0.1	0
Northern Flicker (*Colaptes auratus*)							0.1		0.1	0
Blue Jay (*Cyanocitta cristata*)					0.1				0.1	—
Red-breasted Nuthatch (*Sitta canadensis*)		0.1+		0.1+	0.1+	1.1		0.4	0	1.7
Brown Creeper (*Certhia americana*)		0.6				0.6	0.2	2.1	0.2	3.3
Winter Wren (*Troglodytes troglodytes*)					2.9	2.6	0.1+	0.1+	3.0	2.7

Appendix I
Continued

Common and scientific name	Michel Point		Mirasty Lake		Appleby Bay		Doré Lake		Total	
	1973	1990	1973	1991	1973	1991	1973	1990	1973	1990–91
Golden-crowned Kinglet (*Regulus satrapa*)						0.1	0.9	0.9	0.9	1.0
Ruby-crowned Kinglet (*R. calendula*)		0.1		0.1	0.1		2.6	4.7	2.7	4.9
Hermit Thrush (*Catharus guttatus*)		0.1	1.1	0.1					1.1	0.2
Cedar Waxwing (*Bombycilla cedrorum*)								0.1+	0	0.1
Yellow-rumped Warbler (*Dendroica coronata*)	1.7	2.9		2.3	1.2	2.3	5.1	6.0	8.0	13.5
Swamp Sparrow (*Melospiza georgiana*)				0.1			0.1		0.1	0.1
White-throated Sparrow (*Zonotrichia albicollis*)	0.1	1.1		0.1	1.7		0.4	0.4	2.2	1.6
Dark-eyed Junco (*Junco hyemalis*)		0.1		0.1	0.1		1.3	0.1	1.4	0.3
Irruptive species										
Purple Finch (*Carpodacus purpureus*)					0.1				0.1	0
White-winged Crossbill (*Loxia leucoptera*)	0.1			0.1	0.6	0.1+	0.9	3.4	1.6	3.6
Pine Siskin (*Carduelis pinus*)	0.1	2.3		1.1	2.3	1.7	0.9	3.0	3.3	8.1
Evening Grosbeak (*Coccothraustes vespertinus*)				0.1		0.1	0.1	0.1	0.1	0.3
Year-round residents										
Ruffed Grouse (*Bonasa umbellus*)	0.1+	0.1+		0.6	0.1+				0.2	0.7
Hairy Woodpecker (*Picoides villosus*)		0.1+			0.1+		0.1		0.2	0.1
Three-toed Woodpecker (*P. tridactylis*)								0.1+	0	0.1
Pileated Woodpecker (*Dryocopus pileatus*)					0.1+	0.6			0.1	0.6
Woodpecker species		0.1+						0.1+	0	0.2
Gray Jay (*Perisoreus canadensis*)			0.1		0.1+	0.2	0.9	0.9	1.1	1.1
Black-capped Chickadee (*Parus atricapillus*)	0.6	1.1	0.6	0.6				0.9	1.2	2.6
Boreal Chickadee (*P. hudsonicus*)	0.6			0.6	1.1	1.7	0.9	1.3	2.6	3.6
Total no. of pairs	57.9	39.0	24.9	20.1	44.1	36.3	25.1	33.0		

Note 0.1 denotes visitor in 1973, possible breeder or cluster in 1990/1991; 0.1+ is probable breeder.

Appendix II

Estimated Numbers of Pairs/10 ha at Mafeking, Manitoba Census Sites

Common and scientific name	Novra		Steeprock Bay		Bellsite		Mafeking		Total	
	1972	1992	1972	1992	1972	1992	1972	1992	1972	1992
Long-distance migrants										
Ruby-throated Hummingbird (*Archilochus colubris*)						0.1[a]			0	0
Olive-sided Flycatcher (*Contopus borealis*)				0.1[a]				0.1[a]	0	0
Yellow-bellied Flycatcher (*Empidonax flaviventris*)			0.1				0.1	0.1	0.2	0.1
Alder Flycatcher (*E. alnorum*)		0.1[a]							0	0
Least flycatcher (*E. minimus*)	2.3	6.9		0.1		0.1[a]			2.3	7.0
Great Crested Flycatcher (*Myiarchus crinitus*)	1.7	0.1	0.1	0.1					1.8	0.2
Bank Swallow (*Riparia riparia*)						0.1			0	0.1
Veery (*Catharus fuscesens*)	4.6	5.7		0.2		0.1			4.6	6.0
Swainson's Thrush (*C. ustulatus*)	2.3	5.7	2.5	2.5		0.1[a]	1.7	0.2	6.5	8.4
Solitary Vireo (*Vireo solitarius*)			1.9	0.2	0.7	0.1	1.1	0.9	3.7	1.2
Warbling Vireo (*V. gilvus*)	0.1			0.1					0.1	0.1
Philadelphia Vireo (*V. philadelphicus*)	2.9	1.7		0.6					2.9	2.3
Red-eyed Vireo (*V. olivaceus*)	8.0	16.0		3.2		1.7		0.1[a]	8.0	20.9
Tennessee Warbler (*Vermivora peregrina*)	1.1	1.1	0.2	0.6	0.3		2.3		3.9	1.7
Orange-crowned Warbler (*V. celata*)		0.1							0	0.1
Nashville Warbler (*V. ruficapilla*)		0.1		0.6	0.1	1.7	2.3	0.9	2.4	3.3
Chestnut-sided Warbler (*Dendroica philadelphia*)	0.6	0.6	0.1	0.6		0.9			0.7	2.1
Magnolia Warbler (*D. magnolia*)		0.6	6.3	8.3		0.3			6.3	9.2
Cape May Warbler (*D. tigrina*)		0.1		0.2				0.6	0	0.9
Black-throated Green Warbler (*D. virens*)		0.6	3.8	3.2					3.8	3.8
Blackburnian Warbler (*D. fusca*)			1.3	0.6				0.1	1.3	0.7
Palm Warbler (*D. palmarum*)						0.2			0	0.2
Bay-breasted Warbler (*D. castanea*)			1.3	0.6			0.6	0.1	1.9	0.7
Black-and-white Warbler (*Mniotilta varia*)	4.0	0.6	0.1	2.5					4.1	3.1
American Redstart (*Setophaga ruticilla*)	19.4	18.0	0.6	6.3					20.0	24.3
Ovenbird (*Seiurus aurocapillus*)	6.3	6.9	1.0	4.4		2.2			7.3	13.5
Northern Waterthrush (*S. noveboracensis*)	1.7	1.1		0.1[a]		0.1[a]			1.7	1.1
Connecticut Warbler (*Oporornis agilis*)				0.1	0.7	0.3		0.9	0.7	1.3
Mourning Warbler (*O. philadelphia*)	0.1	0.6	1.0	0.2					1.1	0.8
Common Yellowthroat (*Geothlypis trichas*)		0.2		0.1			0.6		0.6	0.1
Canada Warbler (*Wilsonia canadensis*)	1.7	8.6	4.1	3.8				0.1[a]	5.8	12.4
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1.1	1.7		0.6		0.1			1.1	2.4
Chipping Sparrow (*Spizella passerina*)			1.0	1.9	3.4	3.4	1.1	1.7	5.5	7.0
Clay-colored Sparrow (*S. pallida*)						0.5			0	0.5
Lincoln's Sparrow (*Melospiza lincolnii*)								0.2	0	0.2

Appendix II
Continued

Common and scientific name	Novra		Steeprock Bay		Bellsite		Mafeking		Total	
	1972	1992	1972	1992	1972	1992	1972	1992	1972	1992
Short-distance migrants										
Mourning dove (*Zenaida macroura*)		0.1[a]				0.1		0.1	0	0.2
Yellow-bellied Sapsucker (*Sphyrapicus varius*)		0.1[a]	0.1						0.1	0
Northern Flicker (*Colaptes auratus*)				0.1[a]			0.1		0.1	0
Blue Jay (*Cyanocitta cristata*)		0.1[a]		0.1[a]		0.1[a]			0	0
Red-breasted Nuthatch (*Sitta canadensis*)			1.9	0.2				0.6	1.9	0.8
Brown Creeper (*Certhia americana*)				0.2			0.3		0.3	0.2
Winter Wren (*Troglodytes troglodytes*)			0.6	1.3			0.3	0.3	0.9	1.6
Golden-crowned Kinglet (*Regulus satrapa*)			0.1	0.6		0.3	1.7	1.7	1.8	2.6
Ruby-crowned Kinglet (*R. calendula*)				2.5	0.1		4.0	3.4	4.1	5.9
Hermit Thrush (*Catharus guttatus*)					1.7	2.4			1.7	2.4
American Robin (*Turdus migratorius*)	0.1					0.1[a]		0.1[a]	0.1	0
Cedar Waxwing (*Bombycilla cedrorum*)					0.7				0.7	0
Yellow-rumped Warbler (*Dendroica coronata*)		0.1	1.3	3.2	2.4	0.7	2.3	2.3	6.0	6.3
Vesper Sparrow (*Pooecetes gramineus*)					0.3	0.1[a]			0.3	0.1
Song Sparrow (*Melospiza melodia*)						0.2			0	0.2
White-throated Sparrow (*Zonotrichia albicollis*)		1.4	1.9	3.5		0.9		0.1	1.9	5.9
Dark-eyed Junco (*Junco hyemalis*)			0.1		1.7	0.3	0.3		2.3	0.3
Brown-headed Cowbird (*Molothrus ater*)	0.1	0.1[a]							0.1	0
American Goldfinch (*Carduelis tristis*)		0.1				0.1[a]			0.1	0.1
Irruptive species										
Purple finch (*Carpodacus purpureus*)	0.1	0.6	0.2	0.1[a]		0.1			0.3	0.7
White-winged Crossbill (*Loxia leucoptera*)		1.1				0.1			0	0.1
Pine Siskin (*Carduelis pinus*)				0.1					0	0.1
Evening Grosbeak (*Coccothraustes vespertinus*)		2.0				0.3		0.1	0	3.1
Year-round residents										
Spruce Grouse (*Dendragapus canadensis*)		0.1		0.1			0.3	0.3	0.3	0.5
Ruffed Grouse (*Bonasa umbellus*)	0.1								0.1	0
Downy Woodpecker (*Picoides pubescens*)	0.6			0.1					0.6	0.1
Hairy Woodpecker (*P. villosus*)		0.6	0.3	1.0		0.3			0.3	1.9
Black-backed Woodpecker (*P. arcticus*)				0.6					0	0.7

Appendix II
Continued

Common and scientific name	Novra		Steeprock Bay		Bellsite		Mafeking		Total	
	1972	1992	1972	1992	1972	1992	1972	1992	1972	1992
Three-toed Woodpecker (*P. tridactylus*)								0.6	0	0.6
Pileated Woodpecker (*Dryocopus pileatus*)				0.6					0	0.6
Black-capped Chickadee (*Parus atricapillus*)	0.1	1.1		0.2	0.2	0.2		0.6	0.3	2.1
Boreal Chickadee (*P. hudsonicus*)			0.1	0.2		0.1	1.1	0.6	1.2	0.9
Gray Jay (*Perisoreus canadensis*)		0.2	0.1	0.6	0.1		0.6	0.3	0.8	1.1
White-breasted Nuthatch (*Sitta carolinensis*)	0.1	0.2							0.1	0.2
Total no. breeding pairs	59.1	83.9	32.1	57.1	12.4	19.2	20.9	17.1		

Note 0.1 denotes visitor in 1972, possible breeding or cluster in 1992; 0.1[+] is probable breeder; [a] = birds recorded at edge of plot, possible visitors or associated with other stand type (excluded from totals).

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NESTS OF NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON

Eric D. Forsman[1] and Alan R. Giese[1]

Abstract.—We located 155 nests in 82 territories occupied by Northern Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula, Washington. All nests were in trees. Of 116 nests that were measured, 105 were in cavities and 11 were in external platforms on tree limbs. Cavity nests were typically in large holes in the side of the trunk or in the broken top of the trunk. Aspect of cavity entrances was non-random, with the majority of cavities facing east-north-east. Location of nest trees did not differ from expected values for slope aspect or position on slope. Proportions of nest sites in different percent slope categories differed from availability, with more nests than expected in the higher percent slope categories. Nests usually were in stands with high overall canopy closure (≥ 70%), but canopy closure in the immediate vicinity of the nest varied from 35–90%. Most nests (87%) were in multilayered stands dominated by large trees. Nests in younger stands were typically in stands where remnant old trees were present. Owls changed nests between successive nesting events in 80% of all cases. Changes in pair members on a territory did not influence the frequency with which pairs switched to a new nest tree in the next nesting year. Based on observed rates of attrition, the expected life span of nests was 120 years.
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Spotted Owls (*Strix occidentalis*) use a variety of structures for nests, including cavities, platforms constructed by other birds or mammals, platforms that are the result of natural accumulations of debris, and ledges on cliffs or cave walls (Bent 1938, Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993). In most regions, nesting is limited primarily to trees (Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993, Folliard 1993). Nesting on ledges on cliffs or cave walls is largely restricted to rocky canyons in the southwestern United States and Mexico (Dickey 1914, Ligon 1926, Bent 1938, Ganey 1988). However, two nests on cliffs have been observed in western Oregon (M. Brown pers. comm., J. Niles pers. comm). Although there have been no studies in which use versus availability of different nest types have been tested, it appears that the types of nests used are influenced by availability and possibly regional differences in climatic conditions.

With the exception of reports by Buchanan (1991) and Buchanan et al. (1993, 1995), relatively little information is available on characteristics of nests used by Northern Spotted Owls (*S. o. caurina*) in Washington. During a long-term study of demographic characteristics of Northern Spotted Owls on the Olympic Peninsula in western Washington (1987–

[1] USDA Forest Service, Pacific Northwest Research Laboratory, 3200 SW Jefferson Way, Corvallis, Oregon 97331, and Dept. of Fisheries and Wildlife, Oregon State Univ., Corvallis, Oregon 97331.

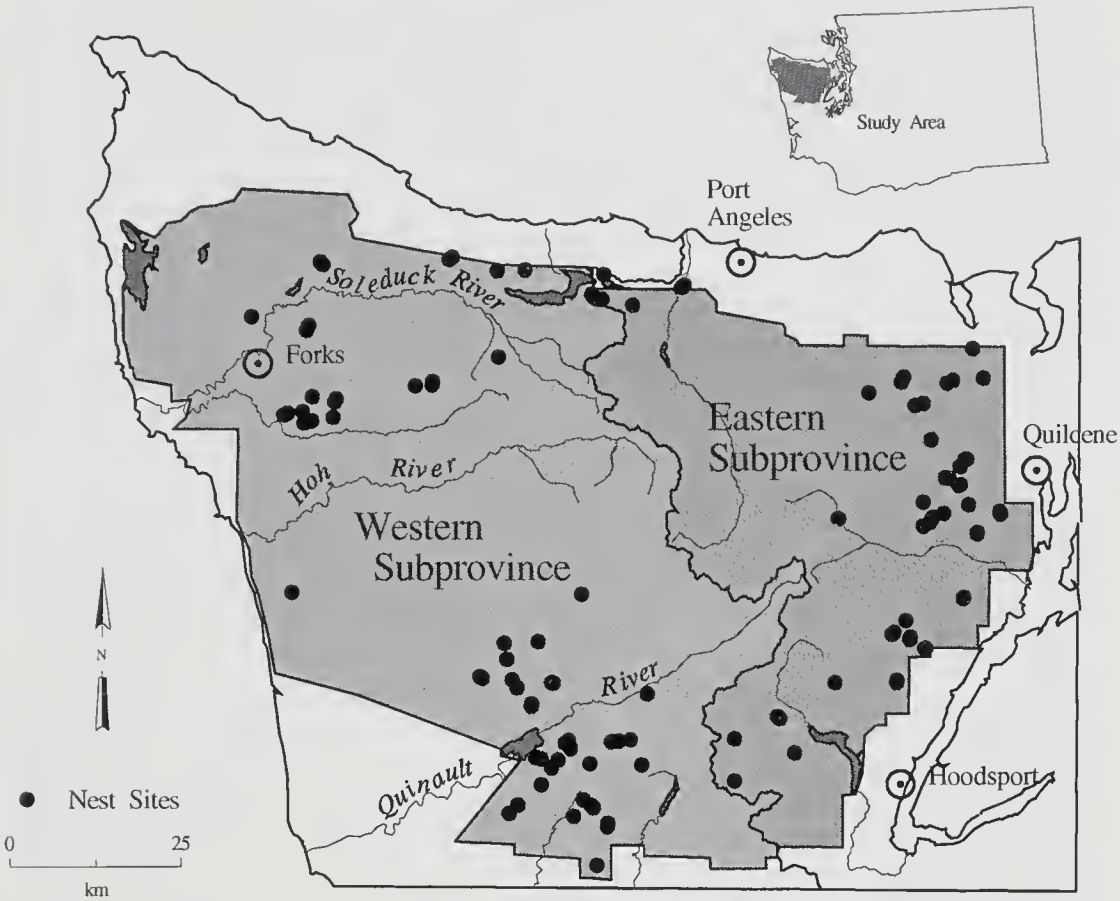

FIG. 1. Location of 116 nest trees used by Northern Spotted Owls on the Olympic Peninsula study area in northwestern Washington. In some cases a single dot may represent more than one nest because nests were very close together. We subdivided the area into western and eastern subprovinces based on differences in precipitation and vegetation.

1994), we located 155 nest trees, some of which were used in multiple years. Herein, we describe characteristics of a sample of those nests, including rates of nest attrition and frequency of reuse of nests.

STUDY AREA AND METHODS

The study area included the entire Olympic Peninsula (Fig. 1). Most field work occurred on lands administered by the USDA Forest Service, but we also monitored some pairs of owls within the Olympic National Park and on lands administered by the Washington Department of Natural Resources. The Olympic Peninsula is a mountainous region characterized by a wet, maritime climate and dense coniferous forests. Mean annual precipitation is highly variable, ranging from 115 cm at Quilcene on the east side of the peninsula (USDA Forest Service records for 1985–1995) to 365 cm on the west side of the peninsula (U.S. National Park Service records for 1987–1992).

Forests on the peninsula are generally dominated by mixtures of western hemlock, (*Tsuga heterophyla*), western redcedar (*Thuja plicata*), sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*) and Pacific silver fir (*Abies amabilis*). Western hemlock, western redcedar, and Sitka spruce predominate in more mesic areas, and Douglas-fir predominates

on drier sites. Pacific silver fir occurs at a broad range of elevations but becomes increasingly dominant at higher elevations.

History of nest use was determined by monitoring the same owl territories each year. Pairs were checked several times each year to determine their nesting status and to locate nest trees. Owls were marked with unique color bands, which made it possible to determine movements between alternate nests and to determine when pair members were replaced by new individuals. Nests were located by observing owls as they carried prey into cavities or platforms (Forsman 1983).

The 155 nests located included 132 on the Olympic National Forest, 13 in the Olympic National Park, four on lands administered by the Washington Department of Natural Resources, five on private lands, and one on the Quinault Indian Reservation. We measured 116 nest trees in 70 territories. The number of nest trees measured per territory was one (33 territories), two (28 territories), or three (9 territories). We climbed 86 nest trees in order to measure dimensions of nest cavities or platforms and measured 30 from the ground, with no nest dimensions taken. Selection of nests for measurement was not random. We simply measured as many nests as we could, incidental to the other objectives of our study. To assess whether types of nests used by spotted owls differed between the wet coastal region of the peninsula and the comparatively drier east slope of the Olympic Mountains, we stratified the study area for some analyses (Fig. 1).

We used a metric tape or clinometer to measure vertical distances. Tree diameter at breast height (DBH) was measured 1.4 m above ground, except that trees with swollen bases were measured immediately above the swelling. Tree diameter at nest height (DNH) was measured at the level of the nest. If the tree had secondary tops, the number of tops was recorded. Secondary tops were limbs that grew upward and formed a new top after the original top of the tree broke off or died. Trees were classified as alive if they had any live limbs, regardless of whether the nest was in a live portion of the tree or not.

Nest types were classified as side cavities, top cavities or external platforms. A side cavity was a hole in the side of a tree trunk. A top cavity was a hole or depression in the broken top of a tree bole that was accessed through the top of the bole. External platform nests were accumulations of sticks or other debris located on limbs outside a tree bole.

Nest entrance width and height were defined as the horizontal and vertical dimensions of the entrance in centimeters. These parameters were measured only for nests with obvious horizontal and vertical entrance limits. Such measures were not applicable to external nest platforms or to cavity nests with large, irregular shaped entrances. Cavity depth was the vertical distance from the cavity entrance to the cavity floor. Platform depth applied only to external platform nests and was the vertical distance from the bottom of the nest structure to the top edge of the structure. Mean diameter of each cavity or external platform was estimated by taking two measurements at right angles to each other across the cavity or platform and dividing the sum by two.

Percent cover above the nest was visually estimated as overhead cover from the perspective of an owl in the nest, including contributions from cavity structure and overhanging vegetation. All estimates of percent cover above the nest were made by the same observer, and were thus not subject to among-observer variation. Entrance aspect was an azimuth from the center of the tree through the center of the cavity opening or across the center of the nest platform (for external nests).

Each nest stand was assigned to one or more structural categories depending on the size distribution of the trees. Categorizations of nest stand structure were based on visual inspection rather than on exhaustive measurements. Canopy closure within a 30 m radius of the nest tree was estimated visually. Elevations were recorded using altimeters or USGS maps. Other variables recorded were slope azimuth, slope gradient (in percent), and position

of nests relative to topographic position on slope (lower third, middle third, upper third). We used χ^2 tests to determine if slope aspect, slope percent, or topographic position of nests differed from what was available (Marcum and Loftsgaarden 1980). Expected values for categories of slope aspect, slope percent, and topographic position were determined from a random sample of 200 30-m^2 grid cells on a digital elevation map of the Olympic National Forest. Aspects were grouped into eight 45° classes, and slopes were grouped into seven 15% classes. The Rayleigh test (Batschelet 1981) was used to test whether azimuths of nest entrances were randomly distributed.

The annual survival rate of nest trees (ϕ) was estimated by calculating the average proportion of known nest trees that survived each year. The estimated mean life expectancy of nest trees from the time they were first located was calculated using the formula $-1/\ln\phi$ (Brownie et al. 1978:204).

RESULTS

We found 155 nests in 82 different owl territories, including 24 territories where pairs nested only once, 19 where pairs nested in two different years, 23 where pairs nested in three years, 11 where pairs nested in four years, and four territories where pairs nested in five years, and one territory where a pair nested in six years. Two pairs nested twice in the same year after initial nesting attempts failed (Forsman et al. 1995). The total number of different nest trees per territory ranged from 1–4. Thirty-three territories had one nest, 29 had two nests, 16 had three nests, and four had four nests. All nests were in trees.

Nest characteristics.—We measured 116 nests in 70 different territories, including 65 nests in 40 territories in the western subprovince of the peninsula and 51 nests in 30 territories in the eastern subprovince (Fig. 1). Of the nests that were measured, 62 (53.4%) were in side cavities, 43 (37.1%) were in top cavities, and 11 (9.5%) were in external platforms. Frequency of use of different nest types differed between the eastern and western subprovinces of the peninsula ($\chi^2 = 19.4$, 2 df, $P \leq 0.001$), with nests in side cavities predominating in the western subprovince (71%), and nests in top cavities predominating in the eastern subprovince (51%). Percent cover directly above the nest averaged slightly higher in the western subprovince than in the eastern subprovince (Table 1) ($t = -2.31$, 92 df, $P = 0.015$).

Nest trees that were measured included 40 western hemlock, 36 Douglas fir, 33 western red cedar, two Pacific silver fir, two grand fir (*Abies grandis*), one Sitka spruce, one western white pine (*Pinus monticola*), and one unknown species. Ninety nests (78%) were in live trees and 26 (22%) were in dead trees. Frequency of occurrence in different tree species did not differ between nests in live trees, and nests in dead trees ($\chi^2 = 1.72$, 3 df, $P = 0.633$).

Of 90 nests in live trees, 67 (74%) were located above the lowest live limb (i.e., in the crown of the tree), and 23 (26%) were located below

TABLE 1

MEASUREMENTS OF NESTS AND NEST TREES USED BY NORTHERN SPOTTED OWLS ON THE OLYMPIC PENINSULA, WASHINGTON, SUBDIVIDED BY PHYSIOGRAPHIC SUBREGION

Variable	E. subregion			W. subregion			Entire sample		
	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE
Nest height (m)	43	23.2	1.72	63	23.5	1.12	106	23.2	0.96
Tree height (m)	44	33.1	2.01	62	46.0	1.29	106	40.6	1.28
Bole height (m)[a]	26	19.6	1.59	54	20.1	0.96	80	19.9	0.82
DBH (cm)[b]	46	107.2	6.31	64	157.7	8.20	110	136.6	5.93
DNH (cm)[b]	30	69.3	4.52	57	105.6	6.00	87	93.1	4.61
No. secondary tops[c]	42	1.0	0.24	62	1.4	0.20	104	1.2	0.15
Avg. nest diameter (cm)	31	43.9	2.40	55	46.3	1.16	86	45.4	1.14
Percent cover above nest	37	82.2	3.00	57	90.0	1.89	94	86.9	1.68
Cavity depth (cm)[d]	24	28.0	8.73	52	10.8	2.16	76	16.2	3.23
Platform depth (cm)[e]	7	21.0	2.05	2	23.5	3.50	9	21.6	1.71
Entrance width (cm)[f]	11	24.0	3.16	40	25.2	1.74	51	24.9	1.51
Entrance height (cm)[f]	7	95.7	51.89	41	88.5	10.29	48	89.5	11.28

[a] Height to first live limb.
[b] DBH and DHN indicate diameter of tree at breast height and nest height, respectively.
[c] Number of live tree tops developing subsequent to the development of the original tree top.
[d] Distance from cavity entrance to floor of cavity.
[e] Distance from top to bottom of external platform type nests.
[f] Entrance dimensions apply to nests in cavities only.

the crown. When both live and dead trees were included, 67 of 116 nests (58%) were in the crown of a live tree. Mean DBH of nest trees was 136.6 cm (SE = 5.93, range = 30–379 cm). On average, total height, DBH and DNH of nest trees were larger in the western subprovince than in the eastern subprovince ($t_{HT} = -5.39$, $P < 0.001$ $t_{DBH} = -4.88$, $P < 0.001$, $t_{DNH} = -4.84$, $P < 0.001$) (Table 1).

When only nests in live trees were included, the majority (83%) of nests in top cavities were in trees with secondary tops. Only 53% of nests in side cavities and 50% of nests in external platforms occurred in trees with secondary tops. When both live and dead trees were included, the percent of nests in trees with secondary tops was 65% for top cavity nests, 44% for side cavity nests, and 50% for external platforms ($\chi^2 = 3.93$, 2 df, $P = 0.140$).

Mean entrance dimensions of cavities were 24.9 cm (width) and 89.6 cm (height) (Table 1). However, entrance dimensions were recorded only for cavities that had well-defined entrances. As a result, our mean entrance dimensions did not represent many cavities that were accessed through large, irregular shaped holes that were formed when tops or large limbs broke off of trees. Nests of the latter type were typically entered through a long crack of variable width in the side of the tree or through the jagged

TABLE 2

MEASUREMENTS OF SPOTTED OWL NESTS IN CAVITIES AND EXTERNAL PLATFORMS ON THE OLYMPIC PENINSULA, WASHINGTON

	Cavity nests			Platform nests[a]			Comparison of means[b]	
Variable	N	$\bar{x}$	SE	N	$\bar{x}$	SE	t	P
Nest height (m)	95	23.3	1.02	11	24.1	3.00	−0.27	0.791
Tree height (m)	95	40.7	1.36	11	39.8	3.99	0.21	0.837
Bole height (m)[c]	70	19.9	0.87	10	20.2	2.66	−0.13	0.896
DBH (cm)[d]	99	141.8	6.15	11	88.7	15.74	2.77	0.007
DNH (cm)[d]	79	97.1	4.74	8	53.4	10.73	2.86	0.005
Avg. nest diamter (cm)	76	45.3	1.15	10	48.0	4.59	−0.76	0.449
Percent cover above nest	83	87.0	1.79	11	86.2	5.02	0.12	0.906
No. secondary tops	94	1.2	0.15	10	1.7	0.75	−0.98	0.332

[a] Platforms on tree limbs.
[b] 2-tailed t-test. Data on percent cover were log-transformed for t-tests.
[c] Height to first live limb.
[d] DBH and DHN indicate diameter of tree at breast height and nest height, respectively.

top of a tree with a broken bole. Entrance dimensions of cavities did not differ between the eastern and western subprovinces ($t_{width} = -0.32$, 49 df, $P = 0.748$; $t_{ht} = 0.14$, 48 df, $P = 0.896$). The distribution of nest cavity entrance azimuths was non-random, with the majority of nests facing east-north-east (mean angle = 72°, SE = 7.5, $r = 0.2021$, $P = 0.038$, N = 94).

Height of the cavity entrance above the cavity floor averaged 16.2 cm (SE = 3.23, median = 4.5 cm) and ranged from 0-66 cm with a single exceptional value of 203 cm (Table 1). In the latter case, the owls accessed the bottom of the cavity by hopping down a ladder-like series of old branch cores that projected into the hollow interior of the tree.

On average, cavity nests occurred in larger trees than external platform nests (Table 2). Variables that did not differ between cavity nests and external platform nests were nest height, total tree height, bole height, percent cover directly above the nest, mean number of secondary tops, and average diameter of nests (Table 2).

The nest substrate in cavity nests typically consisted of a decomposing mixture of wood, bark, conifer needles, twigs, and insect tillings. Small amounts of moss or lichens were sometimes mixed with the debris. In all cases, it appeared that substrate accumulations were the result of decomposition of the interior of the tree and/or debris falling into the cavity. Nests typically contained remains of prey and pellets forming a layer up to 7 cm deep. Eggshell fragments were rarely found in nests except in conjunction with nest failures.

Of 11 nests classified as external platforms, five were old stick nests that appeared to have been built by Common Ravens (*Corvus corax*) or Northern Goshawks (*Accipiter gentilis*), three were on debris platforms on large clumps of deformed limbs caused by dwarf mistletoe (*Arceuthobium* spp.) infections, and three were collections of debris that accumulated where a tree split into multiple tops. The nest substrate in external platform nests was typically a decomposing mixture of tree bark, conifer needles, twigs, lichens, and moss.

Site characteristics.—Of 116 nests measured, 82 (71%) were in forests characterized by multi-layered canopies where the dominant overstory trees were ≥ 100 cm DBH. Twenty-two nests (19%) were in multi-layered forests dominated by 50–99 cm DBH trees that included scattered individuals or patches of large (≥ 100 cm DBH) old trees. Three nests (2%) were in relatively even-aged forests of 50–99 cm DBH trees, and nine nests (8%) were in forests that included a mosaic of small trees (DBH = 13–49 cm) and larger trees (DBH ≥ 50 cm).

Estimated mean canopy closure in the vicinity of the nest tree ranged from 30–95% ($\bar{x}$ = 70%, SE = 1.44, N = 104) and did not differ significantly (t = 1.50, 102 df, P = 0.136) between the eastern subprovince ($\bar{x}$ = 72.6, SE = 2.43, N = 41) and western subprovince ($\bar{x}$ = 68.2, SE = 1.75, N = 63). Of 13 nest sites with estimated canopy closure ≤ 50%, all were in or adjacent to small natural openings in stands that otherwise had high (≥ 70%) canopy closure.

In the western subprovince, 63 of 65 (97%) nest trees were in forests in which the majority of trees in the overstory and understory were western hemlock, and two (3%) were in forests dominated by Douglas-fir. Western redcedar was present in variable numbers in nearly all stands. Sitka spruce and Pacific silver fir were common associates on lowland and upland sites, respectively.

In the eastern subprovince, 37 nests (73%) were in forests in which the majority of trees in the overstory were Douglas fir, and 14 (27%) were in forests dominated by western hemlock. Common associates in Douglas-fir stands were western hemlock, western redcedar, and Pacific silver fir, with the silver fir component generally increasing with elevation. Stands dominated by western hemlock typically included variable amounts of western redcedar, Douglas-fir, and Pacific silver fir. Grand fir (*Abies grandis*) was a relatively uncommon overstory component in a few low-elevation nest sites in the eastern subregion.

In both subprovinces, western white pine, grand fir, red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophylum*) were present in many nest stands, usually in small amounts. Red alder was typically limited to areas along streams or swampy areas.

TABLE 3

PROPORTIONS OF SPOTTED OWL NEST LOCATIONS AND RANDOM LOCATIONS IN DIFFERENT PHYSIOGRAPHIC CATEGORIES ON THE OLYMPIC PENINSULA, WASHINGTON, 1987–1994

Variable	Nests[a]	Random	95% CI[b]
Slope aspect			
North	0.108	0.140	
Northeast	0.171	0.105	
East	0.090	0.120	
Southeast	0.126	0.155	
South	0.117	0.125	
Southwest	0.108	0.120	
West	0.144	0.140	
Northwest	0.135	0.095	
Slope gradient (%)			
0–14	0.129	0.140	−0.106, 0.084
15–29	0.086	0.165	−0.168, 0.010
30–44	0.129	0.205	−0.177, 0.025
45–59	0.155	0.210	−0.161, 0.512
60–74	0.216	0.180	−0.076, 0.148
75–89	0.164	0.065	0.006, 0.192
90+	0.121	0.035	0.007, 0.165
Position on slope			
Lower third	0.500	0.450	
Middle third	0.345	0.400	
Upper third	0.155	0.150	

[a] Sample sizes for nest variables were 111 (aspect) and 116 (% slope, slope position). Sample size for random samples was 200.

[b] Ninety five percent confidence intervals are presented only for variables that had significant χ^2 tests for use versus availability. Intervals indicate whether a category was used more than expected (interval is positive), less than expected (interval is negative) or in proportion to availability (interval overlaps 0).

Location of nest trees did not differ from expected values for slope aspect (χ^2 = 5.17, 7 df, P = 0.64) or position on slope (χ^2 = 0.99, 2 df, P = 0.61) (Table 3). Proportions of nest sites in different percent slope categories differed from availability, with more nests than expected in the steeper percent slope categories (χ^2 = 22.61, 6 df, P = 0.001) (Table 3).

Elevation at nest sites ranged from 104–975 m in the western subprovince and 114–1189 m in the eastern subprovince. When nests were grouped into 150 m elevation bands, the distribution of nests differed in the eastern and western subprovinces (χ^2 = 35.6, 7 df, P <0.001, Fig. 2). The proportion of nests above 600 m elevation was 59% in the eastern subprovince, compared to only 10% in the western subprovince. In both regions, upper elevations at which nests were located generally corresponded with the transition to stands that were largely dominated by Pa-

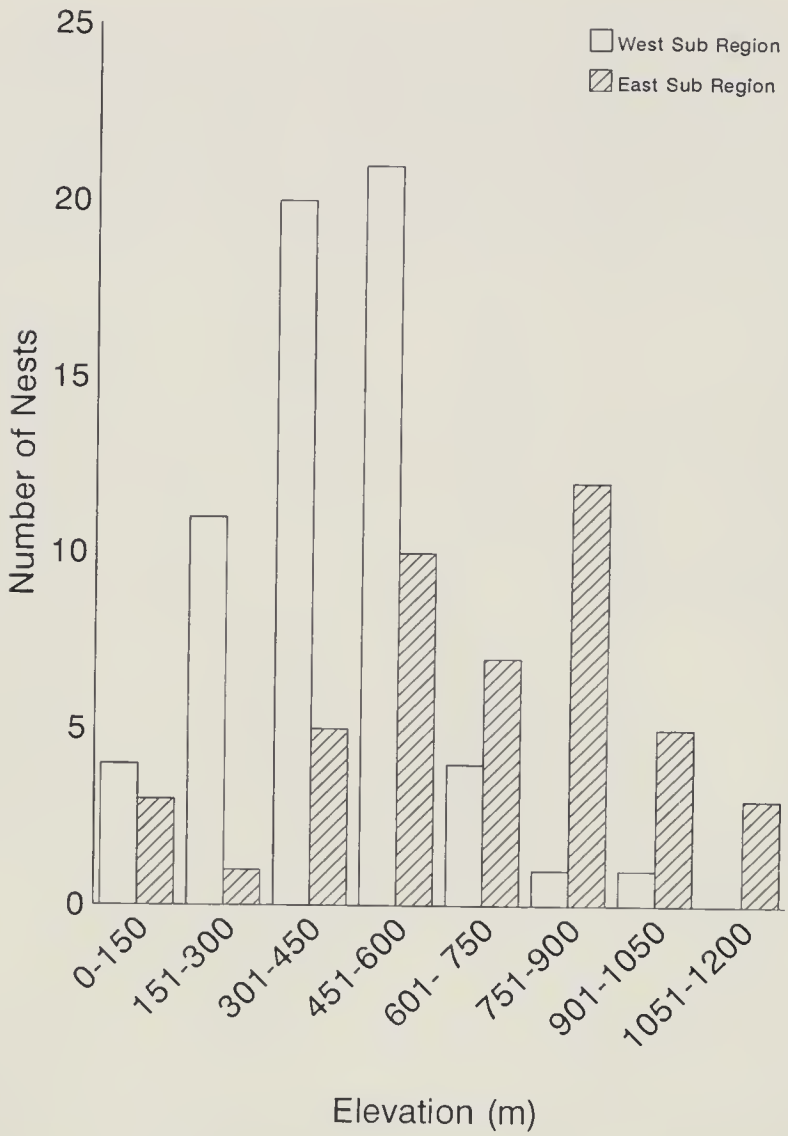

FIG. 2. Distribution of 108 Spotted Owl nests by elevational zone on the Olympic Peninsula, Washington, 1987–1994.

cific silver fir. Due to differences in temperature and precipitation this transition occurred at about 900 m in the western subprovince and 1200 m in the eastern subprovince (Henderson et al. 1989).

Site history.—Of 116 nest trees measured, three became nonfunctional during the study. In two cases, the tree fell down. In one case, the tree remained standing but the cavity collapsed. The average annual survival rate of nest trees from 1987–1993 was 0.992 (SE = 0.003). Estimated mean life expectancy of nest trees from the time they were first located was 124 years.

Although their historical nests were usually still intact, owl pairs changed nests in 88 of 118 (75%) sequential nesting attempts. This calculation was based on the entire sample of 155 nests, and all years of

data for all pairs that nested in ≥ 2 yrs. Frequency of switching to different nests in different years did not differ between pairs that underwent a change in a pair member versus pairs that did not change members (χ^2 = 0.190, 1 df, P = 0.663). Use of a different nest following replacement of a pair member was 80% following a male replacement (N = 10) and 60% following a female replacement (N = 10) (χ^2 = 0.952, 1 df, P = 0.329).

The frequency with which pairs changed nests in sequential nesting years did not differ between 17 cases in which pairs failed at nesting (0.765) and 83 cases in which pairs nested successfully (0.699) (χ^2 = 0.298, 1 df, P = 0.585). This comparison did not include two pairs that failed and renested in the same year. In the latter cases, both pairs moved to a new nest for their second nesting attempt.

At 40 territories where we observed at least two nest change events, we found that at least 40% of the time pairs changed back to a nest that had been used in previous years. The median distance between alternate nests was 0.52 km (range = 0.03–3.36 km, N = 92). At 46 territories where we confirmed two or more nests used in different years, the area of the smallest circle that encompassed all of the known nests ranged from 0.001–8.87 km^2 (median = 0.33 km^2).

DISCUSSION

Species of trees used for nesting on the peninsula were about equally divided among western hemlock (35%), Douglas-fir (31%) and western red cedar (28%). In contrast, some studies in other regions have reported the majority of nests in Douglas-fir (Forsman et al. 1984, LaHaye 1988, Buchanan et al. 1993). In managed stands in California, 35% of nests were in redwoods (*Sequoia sempervirens*), 27% were in Douglas-fir, 17% were in grand fir, and 13% were in hardwoods (Folliard 1993:31). The considerable variation in species composition of nest trees in different regions suggests that selection is based primarily on the presence of a suitable cavity or platform rather than tree species.

The proportion of nests in dead trees on the Olympic Peninsula (23%) was higher than has been reported from study areas in Oregon (4%), the Washington Cascades (12%), and managed stands in northern California (10%) (Forsman et al. 1984:31, Buchanan et al. 1993:5, Folliard 1993: 30). We do not know if this reflected a difference in the relative abundance of suitable nests in live vs. dead trees, or was due to other factors.

The proportion of nests in external platforms on the Olympic Peninsula (10%) was considerably lower than has been reported for other regions. For example, external platform nests comprised 19% of nests in samples from western Oregon (Forsman et al. 1984:32), and 50–80% of nests in

samples from the east slope of the Cascades in Oregon and Washington (Forsman et al. 1984:32, Buchanan et al. 1993:5). It is unclear whether the high proportion of nests in cavities on the Olympic Peninsula is simply a function of availability. An alternative hypothesis is that Spotted Owls on the Olympic Peninsula actually select for cavity type nests because they provide more protection from the frequent heavy rains that occur during the nesting season.

Availability of different nest types does appear to influence nest selection by Spotted Owls (LaHaye 1988, Folliard 1993). Folliard (1993:51) noted that "Generally, platform nests tended to be used more often in even-aged stands with few or no residual trees remaining." On the east slope of the Washington Cascades, where many stands had been thinned to remove large old trees, 80% of nests examined by Buchanan et al. (1993) were in platforms. These observations suggest that, where large trees with cavities have been removed or are otherwise lacking, and where heavy precipitation is not a common occurrence during the nesting season, platform nests provide a viable alternative for Spotted Owls, if adequate numbers of platforms are present.

Without some sort of overhanging cover, nests in the top of broken off trees are likely to be more exposed to the elements than nests in side cavities. Therefore, we hypothesized that the proportion of nest trees with secondary tops should be higher for nests in top cavities than for nests in side cavities. Although there appeared to be a trend in this direction, the differences were not significant. Thus, while Spotted Owls do appear to select nests with good overhead cover on the Olympic Peninsula, the presence of secondary tops does not appear to be a reliable indicator of this.

Mean nest tree height, nest height, and nest tree dbh on the Olympic Peninsula were about the same as, or slightly greater than, was reported for Oregon and northern California (Forsman et al. 1984, LaHaye 1988, Folliard 1993), but were considerably greater than values reported for the east slope of the Cascades in Washington (Buchanan 1991, Buchanan et al. 1993). The considerable variation in these parameters among regions suggests that size of the tree or height of the nest are relatively less important in nest selection than the presence of a suitable cavity or platform.

Forsman et al. (1984) noted that cavity nests used by Spotted Owls in Oregon tended to be in the upper two-thirds of the canopy while platforms tended to be in the lower third. Buchanan et al. (1993) noted that cavity nests on the east slope of the Cascades were located at all levels in the forest canopy, whereas most platform nests were in the lower third of the canopy. In our sample, nests were found at all levels in the forest canopy,

but the majority of both cavity nests (88%) and platform nests (82%) were in the lower two-thirds of the canopy. We do not know if this reflected selection by the owls or simply reflected the availability of nests. However, the preponderance of platform nests in the lower two-thirds of the canopy is likely explained by availability; large limbs capable of supporting large platform nests tend to be located in the lower part of tree boles, and debris platforms tend to form in the lower canopy as a result of materials falling from above.

Selection for cavities that opened to the east-northeast could possibly be explained by the fact that storms on the Olympic Peninsula typically approach from the west-southwest. However, since we did not have data on the actual availability of cavities with respect to entrance aspect, we could not discount the possibility that selection was based on availability.

Mean width of cavity entrances on the Olympic Peninsula was slightly less than in Oregon (30 cm; Forsman 1983:32) and was slightly above the upper end of the range reported by (Folliard 1993:28) for managed stands in northern California (15–23 cm). The smallest entrance we measured was 16 × 18 cm, which is similar to the smallest entrance found in California (15 × 18 cm; Folliard 1993:28). Mean diameter of nests on the Olympic Peninsula (45 cm) is similar to values reported for Oregon (50 cm; Forsman et al. 1984:32) and California 52 cm; Folliard 1993: 28). Folliard (1993) noted that width of the nest platform did not differ according to nest type, a result supported by our observations. Although we recorded one cavity that was 203 cm deep, most cavities used by Spotted Owls are less than 100 cm deep (this study, Forsman et al. 1984). Infrequent use of deeper cavities may be a function of availability or may be because owls find it difficult to climb in and out of such cavities.

The fact that nest sites in our study did not differ from expected values for slope aspect or position on slope suggests that these variables were relatively unimportant in nest site selection on the Olympic Peninsula. Although we found higher than expected proportions of nests on steeper slopes, we are unsure whether this represented selection by the owls. It is possible that the distribution of suitable owl nesting habitat was skewed towards the steeper slope categories as a result of historical patterns of forest management in which harvest on steep, unstable slopes was avoided. In northwestern California, Blakesley et al. (1992) also found no differences between observed and expected values for slope aspect at Spotted Owl nest sites. In contrast to our findings, Blakesley et al. (1992) found no differences between observed and expected values for percent slope at nests and found that owls nested on the upper third of slopes less than expected and nested on the lower third of slopes more than expected. Although they did not have data on the availability of different

slope categories in their study areas, some investigators have compared the distribution of slope azimuths at nests with a uniform distribution (Forsman et al. 1984) or random distribution (LaHaye 1988, Buchanan 1991, Folliard 1993). In these cases, some investigators have found significant differences (LaHaye 1988), while others have not (Forsman et al. 1984, Buchanan 1991, Folliard 1993).

The mean and range of canopy closure at nest sites in Oregon ($\bar{x}$ = 69%, SE = 2.65, range = 35–91) (Forsman et al. (1984:30), were nearly identical to measurements from the Olympic Peninsula ($\bar{x}$ = 70%, SE = 1.44, range = 30–95%). Although canopy closure at nests in Oregon and on the Olympic Peninsula was highly variable, Folliard (1993) and Buchanan et al. (1993) stressed the consistency of high canopy cover at Spotted Owl nest sites in their study areas. We are unsure to what extent canopy closure estimates can be compared among study areas, because estimates may have been influenced by differences in methodology or observers.

In contrast to the low rate of attrition of nests on the Olympic Peninsula, Forsman et al. (1984) noted a relatively high rate of attrition of nest trees in Oregon. Of eight nests that became unusable in the Oregon study, four fell down, three were cut down during logging operations, and one cavity collapsed. Although he did not mention overall attrition rates of nests, Folliard (1993) noted that platform nests in northern California were especially ephemeral in nature.

The tendency of Spotted Owls on the Olympic Peninsula to use different nests in different nesting years contrasts with reports from other regions indicating frequent reuse of the same nests in different years (e.g., Forsman et al. 1984, Ganey 1988). This behavior did not appear to be influenced by turnover of pair members or by success or failure of nests in prior years. We do not know of any obvious factors that should have caused owls on the peninsula to use alternate nests more frequently than owls in other regions.

Habitat selection by spotted owls is likely influenced by a variety of factors, including prey availability, availability of suitable nests and roosts, and presence of escape cover. Use of nest stands by Spotted Owls on the Olympic Peninsula appears to be almost entirely restricted to stands of large trees or younger stands in which there are residual old trees. Retention of small clusters of live trees in harvest units may provide future nesting habitat in stands that would otherwise be uninhabitable by Spotted Owls.

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NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS OF CALIFORNIA SPOTTED OWLS

W. S. LaHaye,[1,3] R. J. Gutiérrez[1] and D. R. Call[1,2]

Abstract.—We evaluated quality of nesting habitat and nest-site selection of an insular population of California Spotted Owls (*Strix occidentalis occidentalis*). We assessed habitat structure for successful and unsuccessful nests from 103 independent territories at three spatial scales, and habitat selection by comparing nest stand structure with identical variables from random points. Fledging success was unrelated to nest type, nest tree, nest stand characteristics, or habitat type. However, nest productivity was greatest in lower elevation oak/big-cone fir habitat (1.7 fledglings per successful nest). Nest stands were characterized by greater variation in tree size, higher canopy closure, and greater basal area of large trees compared with random points. We were able to differentiate consistently between nest and random points using discriminant function models (≈79% correct classification). Our results confirm previous observations that California Spotted Owls will use a variety of habitats, but these habitats are consistently characterized by greater structural complexity compared with available habitat. *Received 24 May 1996, accepted. 30 Sept. 1996.*

Conservation of the Spotted Owl (*Strix occidentalis*) is controversial because of its affinity for economically important, late seral-stage conifer forests (Gutiérrez et al. 1995). Both Northern and Mexican Spotted Owls (*S. o. caurina*, *S. o. lucida*, respectively) are Federally listed threatened species because of past and projected habitat loss (U. S. Department of Interior 1990, 1993). In contrast, the California Spotted Owl (*S. o. occidentalis*) is not currently under consideration for Federal protection, presumably because it inhabits a variety of habitat types other than late seral-stage conifer forests and there is no evidence for decline in the largest population occurring in the Sierra Nevada (Verner et al. 1992). Nevertheless, at least one insular population of California Spotted Owls is declining rapidly (LaHaye et al. 1994).

Even though California Spotted Owls have been observed in a variety of habitat types, we do not know which of these are preferred habitats. More importantly, we do not know what contribution each habitat type represents to the overall viability of the subspecies. For instance, territorial displacement may force individuals to use less preferred habitats (Van Horne 1983). Individuals in suboptimal habitats may represent sink populations (Pulliam 1988), and while sink populations may help to stabilize a regional population (or metapopulation), they would not be viable by themselves (Pulliam and Danielson 1991).

[1] Dept. of Wildlife, Humboldt State Univ., Arcata, California 95521.
[2] Present address—Dept. of Zoology, Washington State Univ., Pullman, Washington 99164-4236.
[3] Present address—P.O. Box 525, Big Bear City, California 92314.

In this study we evaluated habitat selection and habitat quality of an insular population of California Spotted Owls. We incorporated measures of fitness (reproductive success and productivity) to evaluate the relative quality of habitat characteristics and different habitat types that the owls were using. We also evaluated habitat selection by comparing owl nest stands to random points throughout the San Bernardino Mountains.

STUDY AREA AND METHODS

The California Spotted Owl occurs as insular populations in southern California (LaHaye et al. 1994) with the largest of these island populations in the San Bernardino Mountains. This mountain range, which is part of the Transverse Range Geologic Province (Norris and Webb 1990), includes a large elevation gradient (800 m to 3500 m) as well as the majority of habitats used by the subspecies throughout its geographic range. Mean annual precipitation ranges from less than 20 cm to more than 100 cm and is strongly influenced by elevation, topography, and rain shadow effects (Minnich 1988). The vegetation is diverse ranging from Mojave Desert scrub (Vasek and Barbour 1977) at lower elevations to alpine (Major and Taylor 1977) on San Gorgonio Mountain. Most Spotted Owls occupy mixed conifer forests between 1000 m and 2500 m elevation.

Owl survey methods.—We located Spotted Owls and assessed their reproductive activity following methods of Franklin et al. (1996). Nests were located by following male owls to nest trees or by observing females leaving or entering nests. To minimize disturbance we did not measure nesting habitat until after juveniles fledged. Nests were classified as platform, cavity or broken-top (LaHaye 1988). Broken-top nests were typically found near the breakpoint of a broken trunk. Cavity nests were usually formed by a large branch tearing free of the main stem. Both of the above nest types required advanced heart rot for proper development. Platform nests were either abandoned stick nests constructed by other animals or natural accumulations of debris in the branches.

Vegetation measurement.—We measured vegetation characteristics using a variable circular plot (Mueller-Dombois and Ellenberg 1974) at nest and random locations. Random points were selected from universal transverse mercator coordinates throughout forest habitat in the San Bernardino Mountains. At nest and random points we estimated basal area of trees using a 20-factor basal area prism (Dilworth 1981). We measured the height and diameter at breast height (dbh) of each tree tallied with the prism. Diameter estimates were then grouped for further analysis with the conifer dbh classes sapling (0.1–25.0 cm), pole (25.1–50.0 cm), medium (50.1–75.0 cm) and large (>75.0 cm). Hardwood dbh classes were similar except we based them on 15 cm intervals instead of 25 cm intervals. We estimated percent canopy closure using a concave, spherical densiometer (Lemmon 1957). Other habitat characteristics were measured using standard techniques (see LaHaye 1988). Nests were also classified by their location in mixed conifer forests above 1800 m (*Pinus jeffreyi*, *P. ponderosa*, *P. lambertiana*, *Abies concolor*), oak/big-cone fir forest below 1500 m (*Quercus chrysolepis*, *Pseudotsuga macrocarpa*) and mid-elevation conifer/hardwood habitat.

Statistical analysis.—We explored differences between successful and unsuccessful nests across three spatial scales. If one or more fledglings were produced at a nest, then it was classified as successful. At the smallest scale, we tested for independence between nest success and both nest type and nest tree characteristics (dbh, nest height, tree height). We then expanded the analysis to nest stand variables and finally we considered patterns of nest success between broad habitat categories. We also evaluated differences in nest productivity

(average number of fledglings/successful nest) at the broadest scale. In order to avoid pseudoreplication, only one nest site per owl territory was used in our analyses. When data appeared normally distributed we used parametric statistics for our comparisons, otherwise nonparametric tests were used. For multiple pairwise comparisons we adjusted our significance level using a 95% Bonferroni interval to avoid excessive Type I error (Neter et al. 1990) and used Tukey's studentized range test for significant ANOVAs. We compared slope aspects (compass bearings) using circular statistics (Batschelet 1981).

In order to examine differences in forest structure, we calculated the standard deviation for all trec dbh measurements at each sample point. This standard deviation was then treated as a random variable and used to examine differences in variability of tree size between nest and random points. We excluded points where less than two trees were present (1 nest and 33 random sites). This is a conservative test of tree structure differences because Spotted Owl sites usually contain more trees than random sites.

We tested Spotted Owl nest-site selection by comparing 29 vegetation variables from nest points with corresponding values from random points. We also assessed our ability to classify Spotted Owl nesting habitat using a series of discriminant function models (DFMs) (Capen et al. 1986, Call et al. 1992). The DFMs were restricted to five variables that were significantly different between nest and random points ($P < 0.002$) and minimally correlated ($r < 0.6$, Spearman rank test; percent slope, percent canopy closure, hardwood basal area, conifer basal area). Using these five variables we constructed a series of 25 nonparametric DFMs based on a randomly selected subsample of nest and random points (approximately 76 of each type). The DFM algorithm used a k-nearest neighbor density function ($k = 20$, SAS 1989). The ability to discriminate between random and nest points was then evaluated by examining the classification rate for the data set used to construct each DFM (cross-validation) and the ability of each DFM to classify correctly the remaining nest and random points (independent points from approximately 25 nest and 221 random sites). Percent correct classification rates were tested for significance using Cohen's Kappa statistic (Titus et al. 1984).

RESULTS

Between 1987 and 1994 we located 216 California Spotted Owl nests at 103 sites occupied by territorial owls. All nests were in trees and the elevation of nest sites ranged from 885 m to 2560 m. We found nests in ten different tree species (71% conifer, 29% hardwood, Table 1) and the majority (59%) of these nests were platforms. For the 103 independent nests (one from each territory) we found that the average Spotted Owl nest was located 16.1 m (standard deviation, $s = 6.9$) above ground in a tree that was 24.4 m ($s = 9.1$) tall with a dbh of 90.8 cm ($s = 27.6$). Platform nests were located in trees having a dbh ($\bar{x} = 75.0$ cm, $s = 34.9$) that was significantly smaller than either cavity nest trees ($\bar{x} = 108.3$ cm, $s = 29.1$) or broken-top nest trees ($\bar{x} = 122.3$ cm, $s = 29.0$, $F = 18.2$, df $= 102$, $P < 0.0001$). No platform nests were found on snags (i.e., standing dead trees), whereas 13.5% of broken-top nest trees and 23.1% of cavity nest trees were snags. Mean slope aspects where nest and random points occurred ($\phi = 348°$, $r = 0.45$, N $= 103$; $\phi = 341°$, $r = 0.23$, N $= 296$, respectively) were not significantly different ($P > 0.05$).

TABLE 1

NEST TREE SPECIES AND NEST TYPE FOR ALL NESTS USED BY CALIFORNIA SPOTTED OWLS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

Tree species	Number of nests (%)	Percent nest types		
		Platform	Cavity	Broken-top
Abies concolor	75 (34.7)	34.5	13.8	51.7
Alnus rhombifolia	3 (1.4)	66.7	0.0	33.3
Calocedrus decurrens	19 (8.8)	89.4	5.3	5.3
Pinus coulteri	1 (0.5)	0.0	100	0.0
P. jeffreyi or *P. ponderosa*	29 (13.4)	58.6	34.5	6.9
P. lambertiana	19 (8.8)	57.9	36.8	5.3
Pseudotsuga macrocarpa	29 (13.4)	34.5	13.8	51.7
Quercus chrysolepis	34 (15.7)	67.6	23.5	8.8
Q. kelloggii	7 (3.2)	0.0	85.7	14.3
Total	216	58.8	24.1	17.1

Thirty-nine percent of the owl territories occurred in higher elevation mixed conifer forests, while 41% occurred in oak/big-cone fir forests. Twenty percent of the territories were in mixed conifer/hardwood habitat (Table 2).

Nest success.—At the two smaller spatial scales (i.e., nest tree and nest stand) we found no significant differences between successful nests (N = 77) and unsuccessful nests (N = 26) (F and χ^2 tests, $P > 0.05$). Nest success also was independent of habitat type ($\chi^2 = 1.7$, df = 2, $P = 0.4$), but productivity was not. We found more juvenile Spotted Owls fledged from nests located in the oak/big-cone fir forests when compared with the mixed conifer and conifer/hardwood forests (Wilcoxon rank test, $\chi^2 = 7.3$, df = 2, $P = 0.026$, Table 2).

Characteristics of nesting habitat.—In general, nest sites were multi-

TABLE 2

HABITAT TYPES AND FLEDGING SUCCESS FOR CALIFORNIA SPOTTED OWL NESTS LOCATED IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

Habitat type	Number of nests (% successful)	Average fledglings per nest (s)[a]	Average fledglings per successful nest[b] (s)
Oak/big-cone fir	42 (81)	1.39 (0.87)	1.72 (0.61)
Conifer/hardwood	21 (67)	0.98 (1.05)	1.46 (0.97)
Mixed conifer	38 (76)	0.95 (0.77)	1.31 (0.58)

[a] Standard deviation.
[b] Nest productivity.

TABLE 3

SUMMARY OF VEGETATION VARIABLES THAT WERE SIGNIFICANTLY DIFFERENT BETWEEN RANDOM POINTS AND CALIFORNIA SPOTTED OWL NEST POINTS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

	Nest points (N = 103)		Random points (N = 296)	
Habitat variable	Mean[a]	% CV[b]	Mean	% CV
Percent canopy closure	79.3	22.3	52.4	49.9
Percent slope	54.2	49.8	32.1	68.7
Broken-top tree basal area[c]	2.9	174.3	0.5	322.9
Snag basal area	4.8	116.7	1.8	217.8
Hardwood basal area (30.1–45 cm dbh)	3.2	216.7	0.9	332.8
Hardwood basal area (>45 cm dbh)	4.9	144.7	0.8	380.4
Total conifer basal area	37.1	59.5	20.1	85.8
Conifer basal area (50.1–75 cm dbh)	9.6	100.3	4.9	130.1
Conifer basal area (>75 cm dbh)	19.1	77.4	6.7	124.2

[a] Includes zero values for all variables.
[b] Percent coefficient of variation.
[c] Square meters per hectare.

storied stands composed of both conifers and hardwoods (Table 3). In addition, basal areas for large conifers and hardwoods, broken-top trees and snags were significantly higher in nest stands than in random locations. Nest points had a greater mean standard deviation for tree sizes than random points ($\bar{x}$ = 30.9, s = 11.6, N = 102; $\bar{x}$ = 23.0, s = 12.8, N = 263, respectively; t = 5.6, $P < 0.0001$) showing that nest stands had greater variability in tree sizes.

We were able to differentiate consistently between nest and random points based on our DFMs (Table 4). Overall rates of correct classification were very similar for both cross-validation and independent classification schemes (≈79%, $P < 0.0003$). There was greater variation in the correct classification for independent nests which was not surprising given the smaller sample size for this group (average N = 26; Table 4). Overall variation in correct classification was low (coefficient of variation < 10%).

DISCUSSION

Habitat selection in Spotted Owls has been studied extensively (Gutiérrez et al. 1995). The extent of inference, however, is usually limited in these studies for many reasons (Wolff 1995). For example, logistical and financial constraints of field research often restrict selection studies to small sample sizes (e.g., Solis and Gutiérrez 1990, Carey et al. 1990, Call et al. 1992) and pseudoreplicated designs (e.g., Solis and Gutiérrez

TABLE 4

PERCENT CORRECT CLASSIFICATION RATES FOR 25 DISCRIMINANT FUNCTION MODELS (DFM) COMPARING CALIFORNIA SPOTTED OWL NEST POINTS WITH RANDOM POINTS IN THE SAN BERNARDINO MOUNTAINS, CALIFORNIA (1987–1994)

Type of DFM	Mean percent correct classification (% CV)	Range	N[a]	Kappa
Cross-validation[b]				
Nest	82.6 (3.6)	74.6–87.5	77	
Random	78.2 (6.3)	67.9–86.1	76	
Total	80.4 (3.8)	74.2–85.4	153	0.61*[c]
Independent[d]				
Nest	83.1 (8.8)	71.9–95.7	26	
Random	77.7 (3.3)	73.1–81.7	220	
Total	78.2 (2.8)	74.8–82.7	246	0.35*

[a] Mean sample size; actual sample size will vary slightly between each DFM.
[b] Includes only those points that were used to formulate the DFM.
[c] Proportion of points that are correctly classified over the number of correct classifications expected by chance; *, $P < 0.0003$.
[d] Independent classifications only include points that were not used to formulate the DFM.

1990, Call et al. 1992). Habitat studies rarely account for temporal variation and the scale of investigation is usually limited to one or two spatial scales (e.g., Lemkule and Raphael 1993, Hunter et al. 1995). Habitat studies rarely include a full range of available habitats (i.e., include extremes). Finally, habitat quality is rarely assessed using some measure of fitness (Van Horne 1983).

We investigated habitat selection in an entire population of Spotted Owls over eight years at several spatial scales. Our extensive survey efforts have allowed us to sample 95% of all territories consistently in the San Bernardino Mountains each year since 1989 (LaHaye et al. 1994) which includes all habitat types used by the owls. The extent of our sampling avoided pseudoreplication and allowed us to evaluate two measures of fitness (reproductive success and productivity) as indicators of habitat quality.

Nest-site selection.—Spotted Owls selected large trees in which to nest which is consistent with observations throughout their range (LaHaye 1988, Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Seamans and Gutiérrez 1995). Owls in our study also differentially used platform structures as nest sites. The use of platform nests, however, does not appear to be related to nesting success. Thus, selection for nest type may be related to availability of the different nest types; something which we were unable to estimate (see also LaHaye 1988).

Nest habitat characteristics.—Spotted Owls in our study showed a pat-

tern of habitat selection similar to other populations where the owls selected habitats with a structure different than what was generally available to them (e.g., Solis and Gutiérrez 1990, Bias and Gutiérrez 1992, Gutiérrez et al. 1992). Nest sample points were characterized by more complex vegetative structure (greater variation in tree sizes, larger trees, higher canopy closure). Our DFM models demonstrated that the multivariate distribution of habitat characteristics for nest and random points were quite dissimilar. Some overlap, however, is evident between these distributions as we would expect since some random points were in fact suitable owl habitat in terms of stand structure. Of course, it was not possible to determine which of these characters, if any, was the reason for habitat selection. Nevertheless, it appeared that the Spotted Owls were behaving as habitat specialists at the scale of nest habitat selection.

Habitat quality.—Spotted Owls were equally likely to fledge juveniles in all three habitats, but breeding owls located in the lower elevation oak/big-cone fir habitat produced more fledglings per nest. This is consistent with earlier reports that showed a negative relationship between productivity and elevation (Bart and Forsman 1992). Given the potential for improved fitness in the oak/big-cone fir habitat, we would predict that owls would select this habitat preferentially. This appears to be the case; Smith (1995) estimated the ecological densities for this same population to be 0.43, 0.20 and 0.11 owls/km^2 for oak/big-cone fir, conifer/hardwood, and mixed conifer, respectively. Higher densities may reflect smaller territory sizes which could result from increased prey densities associated with higher mast production at lower elevations. Thus, owls may have more energy to invest in reproduction in the lower elevation oak/big-cone fir habitat. Ultimately, we will need data on survivorship and reproductive success of fledglings from each of these habitat types before we can assess their true contribution to the total population of California Spotted Owls in the San Bernardino Mountains.

There is a potential for increased disturbance of Spotted Owl habitat associated with the burgeoning human population in southern California (McKelvey and Weatherspoon 1992). In particular, as demand for housing and general suburban expansion continues in San Bernardino County, the lower elevation oak/big-cone fir habitat may be the first to be impacted. Smith (1995) has shown a strong negative association between habitat fragmentation and occurrence of Spotted Owls. Thus, human disturbance is likely to fragment these important habitats and negatively affect what appears to be the most productive segment of the San Bernardino Spotted Owl population.

We infer from our study results that although Spotted Owls used a variety of habitat types, they selected forests that were different from

available habitat. Further there appears to be differential fledgling productivity attributable to different habitats, but not to nest structure *per se*. Therefore, we conclude that Spotted Owls are structural habitat specialists inhabiting areas of differing qualities.

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AGE-RELATED TIMING OF MIGRATION: GEOGRAPHIC AND INTERSPECIFIC PATTERNS

MARK S. WOODREY[1] AND C. RAY CHANDLER[2]

ABSTRACT.—Differential timing of passage by age or sex classes at sites along migration routes is ambiguous with respect to whether these groups differ in onset or rate of migration and provides little insight into the dynamics of differential timing. Therefore, we compared age-specific differences in timing of autumn migration by five species of passerines at three sites in eastern North America. Two species showed consistent differential timing of migration at all sites, with adults preceding immatures in Red-eyed Vireos (*Vireo olivaceus*) and immatures preceding adults in Magnolia Warblers (*Dendroica magnolia*). Age differences in timing of passage by Swainson's Thrushes (*Catharus ustulatus*), American Redstarts (*Setophaga ruticilla*), and Common Yellowthroats (*Geothlypis trichas*) varied with year and location. The degree of differential timing varied substantially among sites within species. For Swainson's Thrush and Magnolia Warbler, species which breed largely to the north of all three sites, there was little evidence for differential rate of migration between age classes. Only the Red-eyed Vireo and Magnolia Warbler showed evidence of differential onset of migration. Our results point to the need for further data on the dynamics of differential timing as a prerequisite for testing hypotheses on the causes of differential migration. *Received 1 Dec. 1995, accepted 1 Sept. 1996.*

Differential migration among individuals of the same species may involve differences in migratory timing (review by Gauthreaux 1982), distance migrated (reviews by Gauthreaux 1982, Ketterson and Nolan 1983), or both (e.g., Chandler and Mulvihill 1990a, Nolan and Ketterson 1990). Because ornithologists have a long tradition of quantifying the timing of passage by migrants at sites along migration routes, patterns of differential timing are particularly well-known. Differential timing may occur between sexes (e.g., Annan 1962, Johnson 1965, Bildstein et al. 1984, Francis and Cooke 1986, Chandler and Mulvihill 1990a), between recognizable age classes (e.g., Johnson 1965; Hussell et al. 1967; Hussell 1980, 1991; Bildstein et al. 1984; Chandler and Mulvihill 1990a), or among populations of different geographic origin (e.g., Mueller et al. 1981, Högstedt and Persson 1982, Hedenström and Petersson 1984).

Most studies of differential timing in passerines have documented differences in the timing of passage at a specific site. Unfortunately, timing of passage at a single site along the migration route is ambiguous with respect to whether groups (ages, sexes, or populations) differ in onset of migration, rate of migration, and/or site of origin (Chandler and Mulvihill 1990b). Nevertheless, data on the processes that underlie patterns of dif-

[1] Mississippi Museum of Natural Science, 111 North Jefferson St., Jackson, Mississippi 39202.
[2] Dept. of Biology, Georgia Southern Univ., Statesboro, Georgia 30460.

ferential timing are needed to identify the causes of differential timing—causes that have received remarkably little attention despite the recent revitalization of interest in avian migration.

The purpose of this paper is to explore patterns of age-specific differential timing of migration in several species of passerine birds and to discuss the processes that may account for these patterns. Specifically, we quantified geographic (three sites in eastern North America), interspecific (five species), and temporal (two years) patterns of age-specific differential timing of fall migration. Our objectives were (1) to compare migratory timing of adult and immature passerines among several species of passerine birds, (2) to determine whether these patterns are consistent across space and time, and (3) to assess whether these data can be used to provide information on the onset and rate of migration in species that exhibit differential timing of migration. We show that comparisons of migratory timing over a broad geographic area may provide insights into the mechanics of migratory timing and discuss the importance of this information to an understanding of the causes of differential migration.

STUDY AREAS AND METHODS

Study sites.—We assembled data on the timing of autumn migration from three sites in eastern North America. The most northern site was Long Point Bird Observatory (LPBO; 42°33′N, 80°10′W) on the north shore of Lake Erie, Ontario, Canada. The second site was Powdermill Nature Reserve, field station of the Carnegie Museum of Natural History, in western Pennsylvania (PNR; 40°10′N, 79°16′W). The third and southernmost site was Bon Secour National Wildlife Refuge, located on the western tip of Fort Morgan peninsula in coastal Alabama (FTMN; 30°10′N, 88°00′W). These locations were selected for two reasons. First, these sites (separated by 12° of latitude) lie along a migration route for birds moving out of northeastern North America to the Gulf of Mexico where they may take either a circum- or trans-gulf route into the Neotropics. The timing of passage by birds at these sites should be broadly representative of a variety of Neotropical migrants. Second, daily banding operations at each site provide detailed records of migratory timing. A description of banding operations at LPBO can be found in Hussell (1991) and at PNR in Leberman and Wood (1983). At FTMN, approximately 25 12-m mist nets were opened daily throughout the autumn migration in forest and scrub habitat (Woodrey 1995).

Data collection.—We selected five species for analysis: Swainson's Thrush (*Catharus ustulatus*), Red-eyed Vireo (*Vireo olivaceus*), Magnolia Warbler (*Dendroica magnolia*), American Redstart (*Setophaga ruticilla*), and Common Yellowthroat (*Geothlypis trichas*). We chose these five species because identifiable age classes were captured in relatively large numbers at all three banding sites.

Birds included in the analysis (first captures only) were captured at each site during daily banding operations in autumn 1990 and 1991. Capture dates for the five species were 1 Aug.–17 Oct. at LPBO, 1 Aug.–19 Oct. at PNR, and 31 Aug.–31 Oct. at FTMN. Birds of these five species banded over these dates were considered migrants; we assume that any captures of local breeders were insufficient to affect our conclusions concerning differential timing of migration.

For those species whose breeding ranges lie largely to the north of all three capture sites

(Swainson's Thrush and Magnolia Warbler), we estimated average migration rates for adults and immatures based on the median capture dates of each age class at the three sites. This was done by dividing the distance between two sites by the number of days difference in median passage dates at the two sites (Ellegren 1990). These estimates are meant to be qualitative, since they are based on the assumption that the populations of these species sampled at LPBO and/or PNR were at least partially the same as those at FTMN. In short, we assume a simple NE-SW oriented migration route from LPBO and PNR to FTMN and into Central and South America. Although alternative migratory patterns are conceivable, our approach is to make an explicit simplifying assumption and generate testable generalizations about migration rates in the age classes of these two species. This method (comparison of median capture dates from sites along the migration route) has produced estimates of migration speed that compare favorably with rates calculated from direct banding recoveries (Ellegren 1990). The distance from LPBO to FTMN was calculated to be 1610 km; PNR to FTMN is 1380 km.

Statistics.—We used Mann-Whitney tests to compare differences in the capture dates (Julian dates) of adults and immatures at each of the three sites. The Mann-Whitney test is sensitive to differences in the location of the distributions of capture dates between age classes (Sokal and Rohlf 1995). All tests were two-tailed, and we used SYSTAT for all analyses (Wilkinson 1989).

We used box plots for the visual display of migratory timing. These plots convey substantial information about the shape of a distribution by displaying the median with a vertical line, the interquartile range (IQR; a box around the median), and adjacent values (extent of a horizontal line). The upper adjacent value is the observation less than or equal to the upper quartile value plus 1.5 × IQR. The lower adjacent value is the observation greater than or equal to the lower quartile value minus 1.5 × IQR. Observations that lie 1.5 IQRs or 3.0 IQRs beyond the quartile values are outside values and are shown with asterisks and open circles, respectively.

Because we conducted multiple tests (five species at three sites), we sequentially Bonferroni-adjusted (Hochberg 1988) p-values to maintain an experimentwise error rate of 0.10 within years (Chandler 1995). In 1990, all p-values that were significant when unadjusted, remained so after Bonferroni adjustment. In 1991, only two unadjusted values became nonsignificant after adjustment for multiple tests. Therefore, we report unadjusted values and indicate cases where adjustment for multiple tests would alter significance.

RESULTS

Swainson's Thrush.—In 1990, Swainson's Thrushes showed no significant difference in the timing of passage of adults and immatures at LPBO ($U = 8145$, $P = 0.46$), PNR ($U = 685$, $P = 0.09$), or FTMN ($U = 619$, $P = 0.14$) (Fig. 1). The same was true for 1991, with the exception of LPBO, where median passage of adults was significantly earlier than immatures ($U = 13{,}755$, $P = 0.002$; Fig. 1).

The general lack of significant age differences in passage of Swainson's Thrushes among sites suggests that migration rates of adults and immatures were similar (or do not differ sufficiently to result in differential passage over the range of latitudes analyzed here). Nevertheless, the age difference in median dates of passage varied from immatures preceding adults by 4.5 days at FTMN in 1990 to no difference at LPBO in 1990

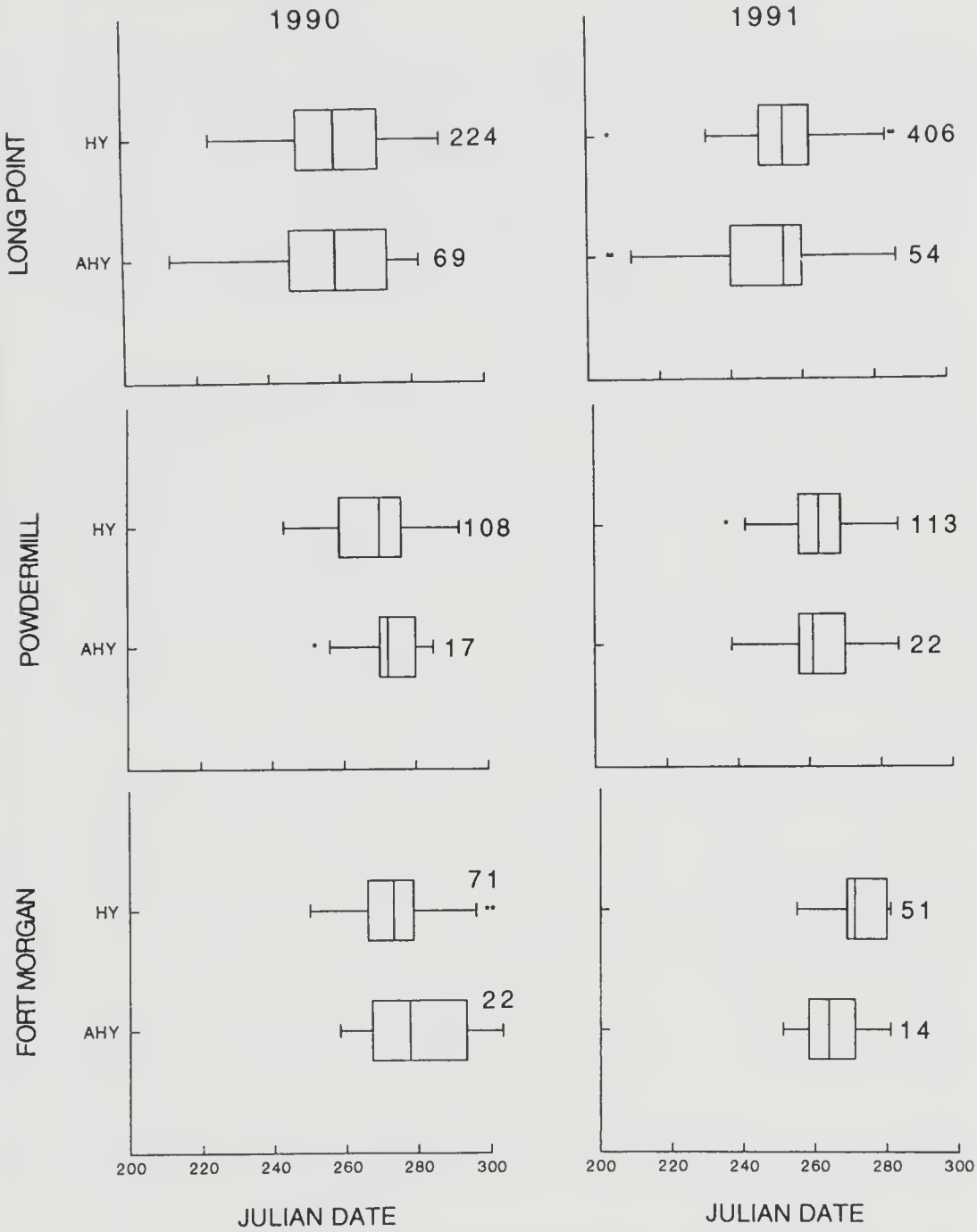

FIG. 1. Distribution of capture dates (first captures only) for Swainson's Thrushes at the three sites. Box plots display median (vertical line within box), interquartile range (extent of box), adjacent values (extent of horizontal line), and outside values (asterisks and open circles). Julian dates range from 18 July (200) to 26 October (300). Sample sizes are given to the right of each plot.

to adults preceding immatures by 7.5 days at FTMN in 1991 (Fig. 1). Passage dates at LPBO (averaged across years) suggested an average migration rate to the Gulf coast of 119 km/day for adults and 108 km/day for immatures. At PNR (again averaged across years), the estimates of migration rates were 402 km/day for adults and 317 km/day for immatures. The large difference in estimated migration rates from LPBO and PNR was attributable to a large difference in passage dates of Swainson's Thrushes at these two sites (7–13 days later at PNR even though these sites are separated by only 235 km).

Red-eyed Vireo.—Adult vireos migrated significantly earlier than immatures at all three sites in 1990. Median passage dates of the age classes differed by 21 days at LPBO ($U = 917$, $P < 0.001$), 22 days at PNR ($U = 8766$, $P < 0.001$), and 17 days at FTMN ($U = 1065$, $P = 0.004$) (Fig. 2). The age differences in timing of migration were so large in 1990 that the median passage of adults at FTMN preceded median passage of immatures at LPBO. The pattern was similar in 1991 but less pronounced. Adults preceded immatures by four days at LPBO ($U = 1456$, $P = 0.04$), 13.5 days at PNR ($U = 2256$, $P = 0.001$), and two days at FTMN ($U = 1205$, $P = 0.06$) (Fig. 2). After adjustment for multiple tests, only the PNR difference was significant.

Estimates of migration rates were complicated by the extensive breeding range of this species. Like Swainson's Thrushes, however, there was local variation in passage dates. Even though LPBO is just to the north of PNR, Red-eyed Vireos passed PNR 8–9 days earlier in 1990 and 11-20 days earlier in 1991 (Fig. 2).

Magnolia Warbler.—In 1990, adult and immature Magnolia Warblers differed significantly in timing of passage at all three sites. Immatures preceded adults by an average of 16 days at LPBO ($U = 2204$, $P < 0.001$), 10 days at PNR ($U = 1263$, $P < 0.001$), and 19 days at FTMN ($U = 359$, $P < 0.001$) (Fig. 3). The same was true in 1991, with immatures preceding adults by five days at LPBO ($U = 5259$, $P < 0.001$), 12 days at PNR ($U = 1292$, $P < 0.001$), and eight days at FTMN ($U = 186$, $P < 0.001$) (Fig. 3).

The median passage dates at LPBO and FTMN (averaged across years) suggested average migration rates of 79 km/day for adult Magnolia Warblers and 92 km/day for immatures. Median passage dates at PNR and FTMN gave estimates of 101 km/day for adults and 103 km/day for immatures.

American Redstarts.—In 1990, there were no significant differences in the timing of passage of adults and immatures at LPBO ($U = 1261$, $P = 0.07$), PNR ($U = 1115$, $P = 0.40$), or FTMN ($U = 1287$, $P = 0.91$) (Fig. 4). The

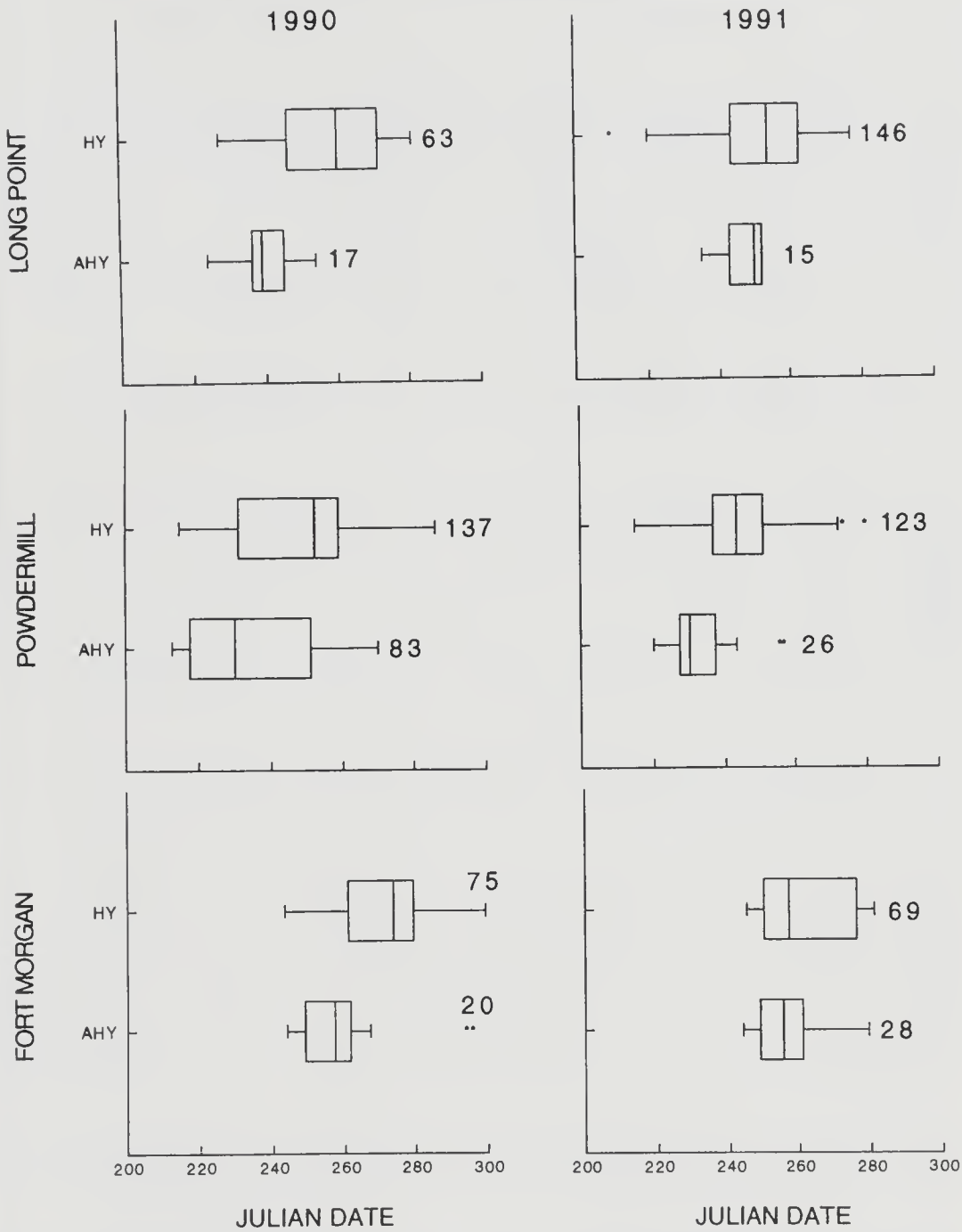

FIG. 2. Distribution of capture dates (first captures only) for Red-eyed Vireos at the three sites. See Figure 1 for description of box plots.

same was true in 1991, with the exception of FTMN where immature redstarts preceded adults by 10 days ($U = 2284$, $P < 0.001$) (Fig. 4).

Although the extensive breeding range of this species complicated inferences about migration rates, there was substantial among-site variation in passage dates. In 1990, the median passage date of adults was 13 days

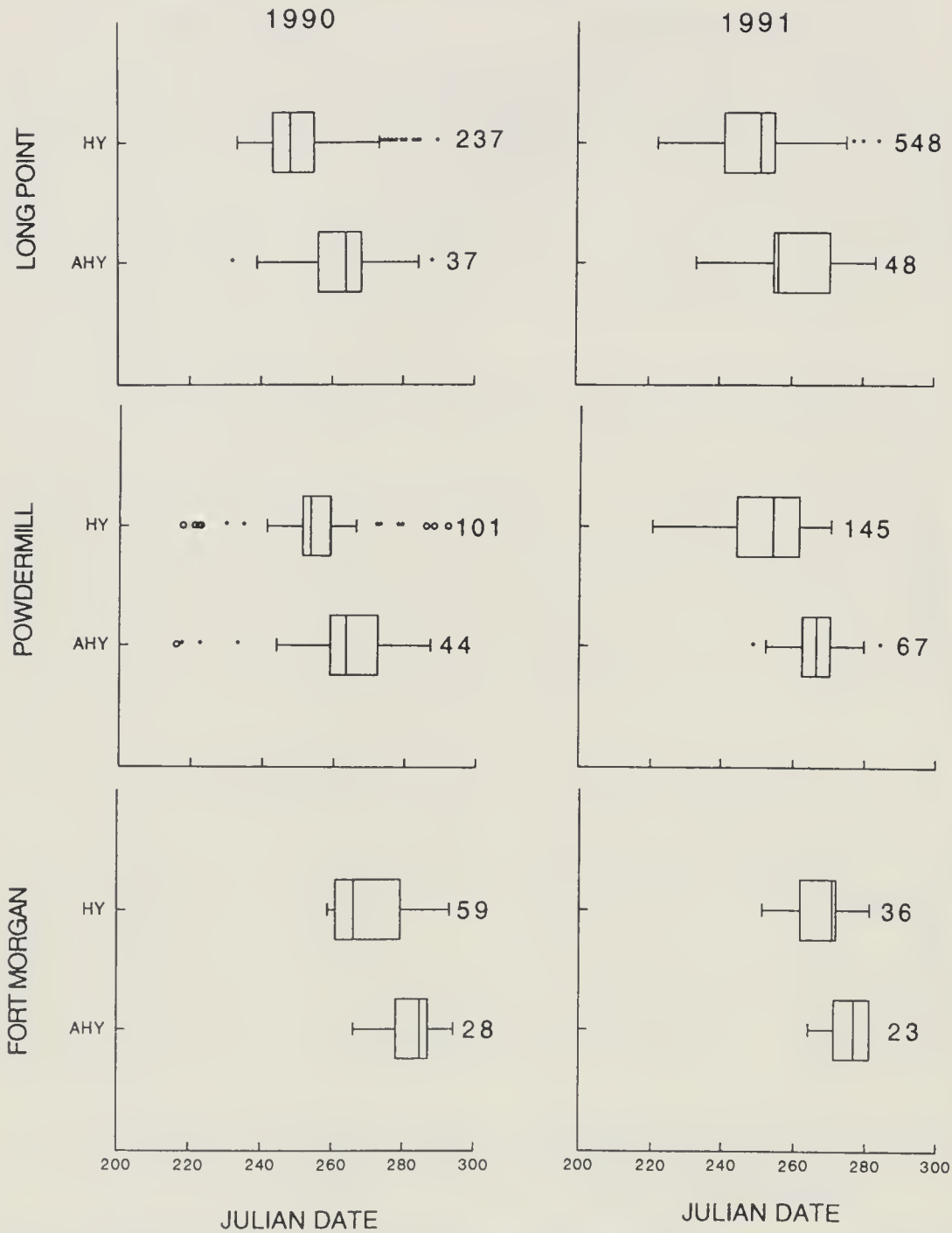

FIG. 3. Distribution of capture dates (first captures only) for Magnolia Warblers at the three sites. See Figure 1 for description of box plots.

earlier at LPBO than at PNR just to the south; the median passage of immatures was only six days earlier at LPBO that same year. In 1991, the median date of passage for the age classes differed by no more than 3.5 days between these two sites (Fig. 4).

Common Yellowthroat.—Adult and immature yellowthroats did not dif-

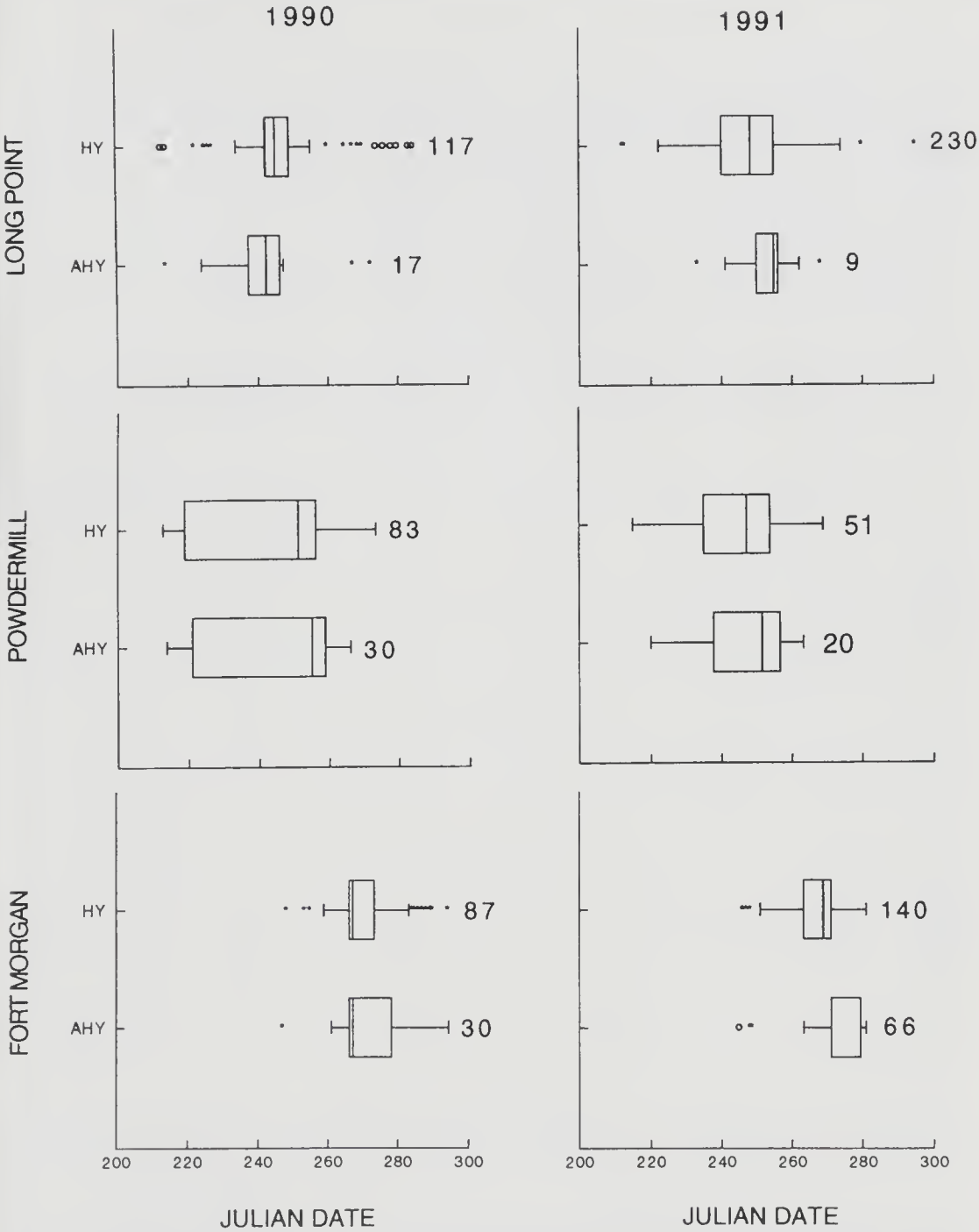

FIG. 4. Distribution of capture dates (first captures only) for American Redstarts at the three sites. See Figure 1 for description of box plots.

fer significantly in timing of passage at any site in 1990 (LPBO: U = 1637, P = 0.14; PNR: U = 7421, P = 0.53; FTMN: U = 1714, P = 0.95) (Fig. 5).

In 1991, median passage of immatures preceded that of adults by 14

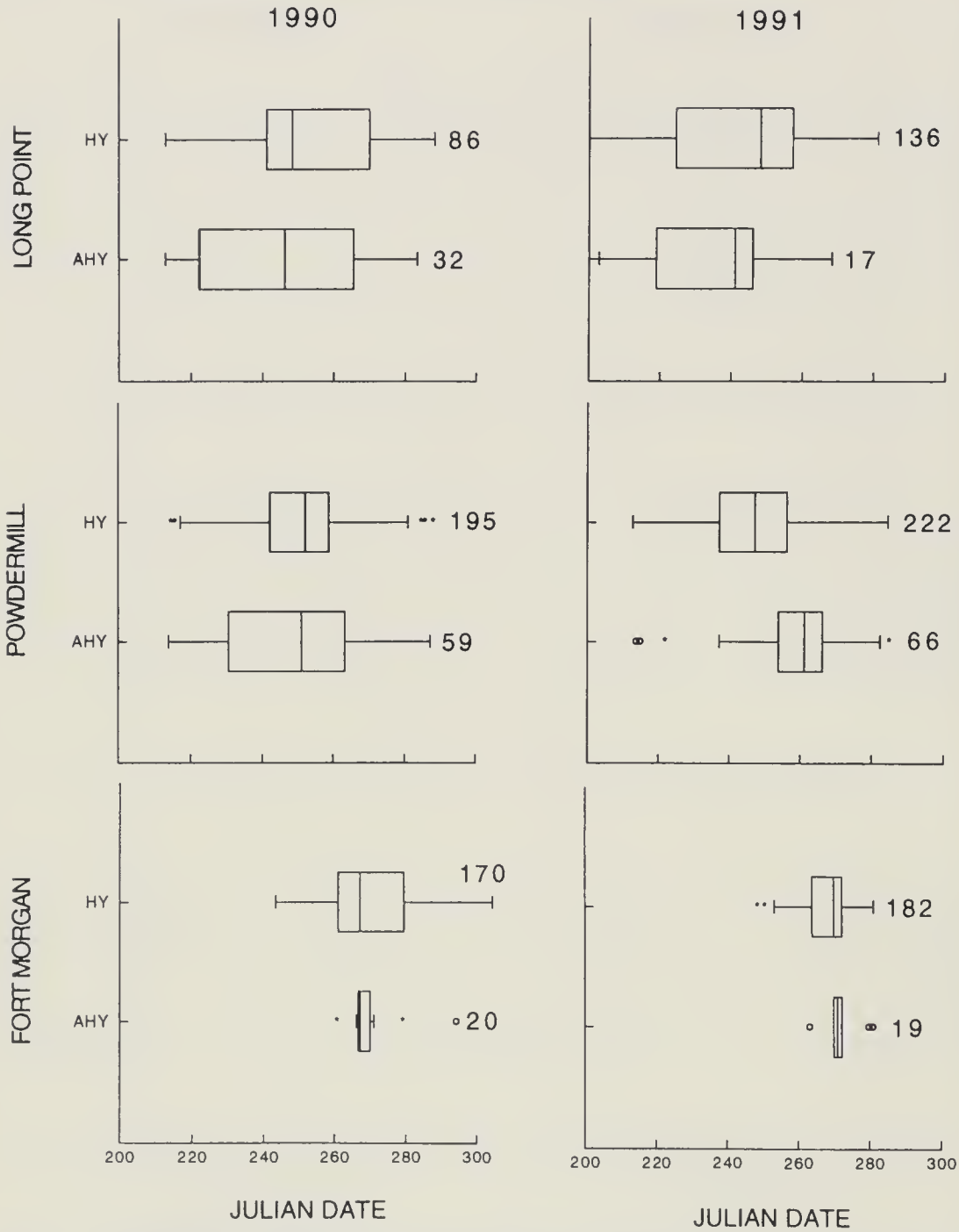

FIG. 5. Distribution of capture dates (first captures only) for Common Yellowthroats at the three sites. See Figure 1 for description of box plots.

days at PNR (U = 3909, $P < 0.001$), but there was no significant differential timing at the other sites (LPBO: U = 1472, P = 0.07; FTMN: U = 1298, P = 0.07) (Fig. 5). In 1991, adult yellowthroats passed LPBO 20 days earlier than at PNR just to the south (immatures had almost identical median passage dates at these sites; Fig. 5).

DISCUSSION

When analyzed on a large geographic scale, five species of passerine migrants showed different patterns of age-specific differential timing of migration. Adult Red-eyed Vireos preceded immatures at all sites, whereas the opposite was true for Magnolia Warblers. Age-specific differences in timing of passage by Swainson's Thrushes, American Redstarts, and Common Yellowthroats varied with site and year. Our results demonstrate that the magnitude of age-specific differential timing can vary substantially between years (e.g., Red-eyed Vireos) and that migratory timing can vary appreciably from site to site within a region (PNR vs LPBO). For those two species for which it was possible to estimate average migration rates, the rates were similar between adults and immatures (Magnolia Warbler) to perhaps faster in adults (Swainson's Thrushes based on PNR data).

The specific patterns of differential timing that we report from each site are not new (e.g., Leberman and Clench 1969, 1970). In fact, many studies document adults preceding immatures during fall migration (e.g., Hussell et al. 1967; Seel 1977; Hussell 1980, 1991; Chandler and Mulvihill 1990a) or immatures preceding adults (e.g., Mueller and Berger 1968, Nilsson 1970, Bildstein et al. 1984). However, simply documenting patterns of differential passage at a site along the migration route offers little insight into the dynamics of differential migratory timing within species of passerine birds (Chandler and Mulvihill 1990b). Comparative analyses of data from several sites along the migration route, such as that attempted here, offer the opportunity to explore the contributions of rate and onset to differential timing in passerines (Rosenfeld and Fagerström 1980, Hildén and Saurola 1982, Ellegren 1990).

Onset versus rate of migration.—Our data provide evidence for differential onset of migration in two of the five species that we examined. Magnolia Warblers showed large age differences in migratory timing at all sites. Because the bulk of their breeding range lies just to the north of LPBO and PNR, differences in rate of migration by age classes of Magnolia Warblers appear insufficient to account for the large differences in their timing of passage at LPBO and PNR. Apparently, immature Magnolia Warblers initiate migration approximately 1–2 weeks earlier than adults, depending on the year. Red-eyed Vireos also show large age differences in timing at all three sites although the magnitude of the difference varied annually. It is difficult to explain this age difference in timing of passage at all sites as a result of age-specific differences in rate of migration. Instead, adult vireos appear to depart the breeding grounds substantially earlier than immatures (possibly as much as three weeks).

This early departure may be related to the fact that adult Red-eyed Vireos show a very limited prebasic molt during late summer (Mulvihill 1993) that might permit earlier onset of migration. A substantial late-summer movement of second-year birds and/or failed breeders (R.S. Mulvihill, pers. comm.) also may be a contributing factor. Whatever the cause, age differences in timing of migration by Red-eyed Vireos appear susceptible to substantial annual variation (Fig. 2).

We also have some evidence on rates of travel by age classes in two of the five species. Assuming that one or both of our northern sites sample the same populations as our Gulf site (or at least populations with the same migratory timing), our results suggest that adult and immature Magnolia Warblers migrate at roughly similar rates (approximately 80–100 km/day). Swainson's Thrushes appear to migrate more rapidly than the warblers, and adults may migrate at a slightly faster rate than immatures (by about 80 km/day based on PNR data). If these age differences are real, they are insufficient to result in significant differential passage by the time Swainson's Thrushes reach the Gulf coast. We emphasize that these estimated rates are based on two seasons of data and are meant to be qualitative, testable generalizations about migratory dynamics within species. Ellegren (1990), in a similar study of Bluethroats (*Luscinia svecica*), found that immatures had slower migration rates than adults early in autumn migration (100 km/day vs 40 km/day) but not as they neared the wintering grounds (immatures approached 100 km/day). Unfortunately, Ellegren's study is rare in reporting age-specific estimates of migration rates in passerines. Our estimated migration rates of 80–130 km/day are generally similar to those reported for other passerines (Hyytiä and Vikberg 1973, Hildén and Saurola 1982, Ellegren 1990). This suggests that our comparisons of timing among sites produced reasonable estimates of migration rates for Swainson's Thrushes and Magnolia Warblers.

The only exceptions to this were our estimates of migration rates by adult and immature Swainson's Thrushes from PNR to the Gulf (402 km/day and 317 km/day, respectively). These large estimates are attributable to Swainson's Thrushes passing PNR almost two weeks later than LPBO just to the north (235 km). The passage dates at LPBO give migration rates for Swainson's Thrushes most similar to those reported in other passerines (Hildén and Saurola 1982), but little is known about movements between these two sites and the Gulf coast. These banding sites may sample different populations of thrushes, or individuals passing PNR could make rapid and direct flights to the Gulf while an ecological barrier at LPBO (Lake Erie) may slow movements or direct birds farther west. That there are interesting migratory dynamics at these sites is further suggested by Red-eyed Vireos moving through PNR 8–9 days earlier than

at LPBO (opposite of the pattern in Swainson's Thrushes) and the fact that age classes of American Redstarts and Common Yellowthroats vary substantially in their timing between the two sites.

Causes of differential timing.—A variety of causes might ultimately result in age differences in onset or rate of autumn migration (Table 1). First, differential timing might result from differential constraints operating on age classes. In other words, there is a single optimal migration schedule for all individuals of a population, but constraints operate differentially on adults and immatures. Second, there may be different optimal migration schedules for the age classes even in the absence of any differential constraints on these groups.

Constraints that might influence migration include age-related differences in timing of molt, which could impose different migration schedules (Rimmer 1988, Chandler and Mulvihill 1990a, Ellegren 1990). Molt that is completed on the breeding grounds should primarily influence onset of migration, whereas molt that extends into migration (or occurs en route; Rohwer and Manning 1990, Thompson 1991) could affect rate of migration. Age differences in molt would have to be pronounced to account for the large differences in onset of migration in Red-eyed Vireos or Magnolia Warblers. Nevertheless, adult Red-eyed Vireos have such a limited prebasic molt during fall (Mulvihill 1993) that it might not preclude a very early onset of migration (Cannell et al. 1983), and molt can delay the departure of adults from the breeding grounds by several days in some species of warblers (Yellow Warbler [*Dendroica petechia*]; Rimmer 1988). Molt also appears to hamper fat accumulation by Swainson's Thrushes at stopover sites (Winker et al. 1992). Overall, the possible costs of molt to fat accumulation rates or flight dynamics need to be quantified further before the influence of molt on differential migration can be tested adequately.

Lack of experience may also place important constraints on migratory timing in immature birds. Inefficient foraging, unfamiliarity with stopover sites, or less efficient navigation could all slow onset or rate of migration. However, lack of experience as a general explanation for slower migration in immatures is not well supported (but see Ellegren 1990). Lack of experience does not appear to preclude early departure from the breeding grounds by immature Magnolia Warblers and subsequent rates of migration comparable to adults. Furthermore, in redstarts and yellowthroats, immatures appear to have migratory timing equal to that of adults. Although inexperience is a fundamental feature of birds undertaking their first migration, specific tests of its effects on migratory timing are needed.

Social interactions might also affect migratory timing (e.g., Gauthreaux 1978, Nolan and Ketterson 1990). As was the case for experience, social

dominance needs further testing as a general explanation for age-specific differential timing. Virtually any observed pattern of age differences in timing could be consistent with the constraints imposed by social dominance. Young birds might leave the breeding grounds early to avoid dominant adults or late because reduced access to food in the presence of dominant adults slows fat accumulation. Along migration routes, immatures might move through stopover sites faster or slower for the same reasons. This is not to suggest that social effects on migratory timing are not important. Rather, these effects need to be tested in specific cases and not simply invoked as being consistent with observed patterns. We know of no data on the possible contribution of social interactions to the differential timing reported here.

Onset of migration in adult birds also might be slowed by the energetic demands of late summer breeding activity. This seems most likely in species raising multiple broods into late summer (immatures from early broods could initiate migration while adults are still occupied with breeding activity). Only the Magnolia Warbler showed differential onset of migration consistent with this constraint and this trait is not apparent in this species. We caution that early migration by failed breeders (as is possible in Red-eyed Vireos) might obscure any clear relationship between adult breeding activity and delayed migration. Finally, the well-documented differences in flight morphology between age classes (e.g., Alatalo et al. 1984, Mulvihill and Chandler 1990) might affect flight speeds, flight ranges, or fattening strategies and thus result in differential rates of migration.

In the absence of differential constraints between ages, there might still be differential timing of migration. Even with equal migratory options open to them, selection might still favor age classes departing the breeding grounds, arriving at stopover sites, or arriving on the wintering grounds at different times (Table 1). Although sexual selection for early arrival on the breeding grounds by males is a clear example of such differential selection, the selection pressures for different optimal migration times between ages during the autumn are less obvious. Migration schedules that are tied to late summer exploration in immatures (Ellegren 1990), to age-specific variation in latitudinal distribution (e.g., Ketterson and Nolan 1983), or to habitat segregation on the wintering grounds (e.g., Lynch et al. 1985) are possible sources of differential selection pressure on rates and onset of migration.

Overall, our results show that broad geographic comparisons of migratory timing can provide insight into the dynamics of differential migration. Quantifying onset and rate of migration permits more detailed analyses of migration strategies and narrows the possible causes of differential

TABLE 1

POTENTIAL ULTIMATE CAUSES FOR DIFFERENTIAL ONSET AND RATE OF MIGRATION BETWEEN AGE CLASSES DURING AUTUMN MIGRATION

Onset of migration	Rate of migration
Differential constraints on timing imposed by:	
Molt on breeding grounds	Molt in transit
Experience	Experience
Social interactions	Social interactions
Breeding activity	Morphology
Differential selection for:	
Early arrival (destination, stopover)	Early arrival (destination, stopover)
Early departure (site of origin)	Early departure (stopover)

timing (Table 1). However, testing of specific causes of differential timing between age classes is hampered by a lack of information on age-specific timing of molts, effects of experience on migratory performance, and the role of social dominance in migratory movements. We hope this study and those such as Ellegren (1990) will stimulate increased attention to the dynamics and causes underlying differential timing of migration.

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THE EFFECT OF AGE ON NEST CONCEALMENT AND ITS COMPLIMENTARY EFFECT ON PRODUCTION OF WOOD THRUSH

MARK S. JOHNSON[1]

ABSTRACT.—Declines in Neotropical migratory land birds have been associated, in part, with decreases in productivity attributed to predation. Since those predators that affect offspring production may be visually dominant (i.e., avian), vegetative nest concealment was quantified for Wood Thrushes (*Hylocichla mustelina*) for fifty nests in a Delaware forest fragment in 1992 and 1993. Nest concealment was tested against age of owners (i.e., ASY vs SY) and with fledgling production. Though past studies have found an age-specific difference in per nest fledgling production, no age-specific differences in concealment were found. However, there was a positive relationship between nest concealment and fledgling output, accounting for 38% of the variation for 1992 and 19% for both years. Results from 1993 were not descriptive, since predation events were fewer. These results are consistent with the logic that the variability of predator communities in different habitats offers no adaptive strategies in nest concealment per se. However, birds may be choosing other, more holistic habitat qualities within territories which may offer greater nest concealment as a benefit. *Received 16 March 1996, accepted 20 Sept. 1996.*

Nest predation may be a major factor influencing avian reproductive success (Ricklefs 1969). Choosing the optimal nest site may be critical in habitats where predation rates are high. Additionally, parental age has been positively associated with increased reproductive performance of Wood Thrushes (Johnson 1994, Johnson and Roth, unpub. data) as well as other species (Saether 1990). Whether learned or innate, the ability to reduce predation through the concealment of nests should serve to increase fitness and be favored through natural selection, particularly in habitats where primary predators are choosing prey visually (e.g., corvids, icterids, etc.).

Some nesting criteria have been positively associated with the age of nest owners, including earlier nest initiation, greater yearly nesting attempts, and larger mean clutches (Saether 1990, Johnson 1994). However, the effect of parental age on nest site concealment has not been measured. The present study examines the effect of age on nest concealment in a migratory Neotropical, open-cup nesting species (Wood Thrush: *Hylocichla mustelina*). Past analyses have found fledgling production of Wood Thrushes to be positively associated with age (Johnson 1994, Johnson and Roth, unpub. data).

[1] Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, Delaware 19717.

STUDY AREA AND METHODS

The study site was a 15-ha woodlot (UDW) on the Univ. of Delaware farm in Newark, Delaware. Surrounding UDW on two sides are large fields used for agriculture; one side is adjacent to athletic fields and the other is a four lane highway. It is a relatively mature, mesic hardwood forest fragment with a mix of Coastal Plain and Piedmont elements characteristic of the Middle Atlantic Region (for more detailed descriptions, see Longcore and Jones (1969), Roth and Johnson (1993), and Gorman and Roth (1989)).

The intensive banding, mapping, and nest-monitoring protocol followed annually since 1974 (Roth and Johnson 1993) was used to provide data on location, success, and ownership of nests for the period 1992 and 1993. Ages were determined from previous banding results for returning adults and from rectrix shape for immigrants (Weinberg and Roth 1994). Nests were checked daily and timing when offspring fledged was recorded.

Potential predators of Wood Thrush eggs and young at UDW include Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus branchyrhynchos*), Common Grackles (*Quiscalus quiscula*), gray squirrels (*Sciurus carolinensis*), white-footed mice (*Peromyscus leucopus*), and raccoons (*Procyon lotor*). Garter snakes (*Thamnophis sirtalis*), and black rat snakes (*Elaphe obsoleta*) are uncommon. No chipmunks (*Tamias striatus*) or flying squirrels (*Glaucomys volans*) were found. Nests which failed were investigated for indicators of predator identity (e.g., tracks, teeth marks on bands, nature of nest destruction, etc.).

Roth and Johnson (1993) attribute most of the 32% failure rate for Wood Thrush nests at UDW from 1978–1987 to predation. During the nesting period of 1992–1993, 65% of nests experienced depredation events, although only 35% were total losses (Roth, unpub. data).

Based on daily observations during the extensive monitoring of UDW, the predominant suspected predators were Blue Jays, Common Grackles, and raccoons. In order to address avian predation effects, nests which failed due to mammalian predation (torn apart), observer error, poor construction, and/or adverse weather were eliminated in the regression analyses so as to only include nests which had the potential to be affected by avian predators.

To calculate nest concealment we quantified cover around each nest, using a "density board" of clear plexiglass bearing a 3 × 4 grid of twelve 4 × 4 cm squares (Fig. 1), immediately following nest abandonment. With the grid centered on the nest and 0.5 m from it, the observer, 3 m away and at eye level with the nest, estimated the proportion of each square that was obscured by vegetation (e.g., 1.0 = totally concealed, 0.3 = ⅓ concealed, etc.). Only vegetation between the density board and the plane passing through the approximate center of the nest, parallel to the board, was considered. Measurements were recorded from the four major compass headings and from directly above the nest. The latter was accomplished using the same grid configuration mounted on an adjustable mirror. Again, as we estimated cover, the grid was 0.5 m from the nest and our eye at nest level. Concealment of each nest was the sum of all measurements at that nest. Since the intent of this study was to address concealment from avian predators, concealment from below was not considered. Since females alone build the nest (Brackbill 1958), concealment values for SY and ASY females were tested initially with a *t*-test. However, to address the possibility that males may be involved in nest site selection and since territories include vegetative characteristics which may be involved in territory selection, male age was also tested. To test if concealment affected nest success, I regressed fledgling production on concealment.

My technique logistically restricted my sampling to nests < 4 m above ground. Owners of nests < 4 m and > 4 m in 1992 and 1993 did not differ in age (females, $\chi^2 = 1.286$, df = 1, N = 113, $P > 0.25$, males $\chi^2 = 1.745$, df = 1, N = 115, $P > 0.18$).

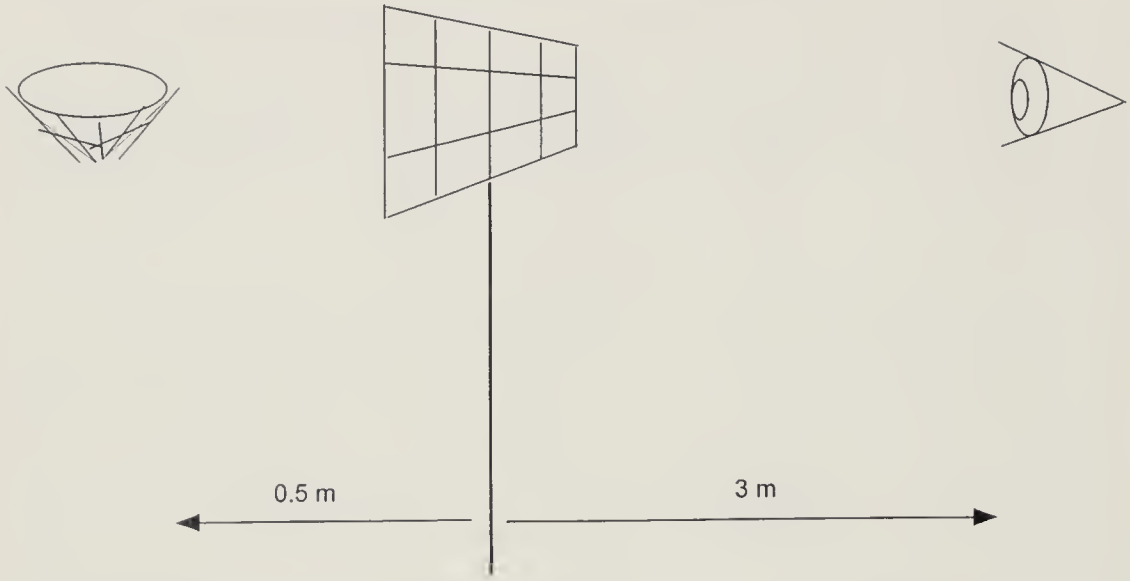

FIG. 1. Diagram of the relative position of nest, observer, and cover density board for estimating vegetative nest concealment.

RESULTS

Vegetational concealment of nests did not differ between SY and ASY females ($\bar{x}$ ASY = 28.5 ± 1.6; $\bar{x}$ SY = 27.25 ± 1.67; $P > 0.95$). Observation of pre-nesting activities (Brackbill 1958) and of multiple use of same nesting sites for territorial males coupled with different females (M. Johnson, pers. obs.) have provided circumstantial evidence that males may influence female nest site selection. As with females, no age class differences were found ($\bar{x}$ ASY = 25.60 ± 1.30; $\bar{x}$ SY = 27.13 ± 1.27; $P < 0.16$). These comparisions included all nests regardless of outcome.

Though there were no relationships between age of parent and nest concealment, a benefit of greater fledgling productivity may be realized from nests with greater concealment. Linear regression of fledgling production on total concealment explained 19% of the variance ($r^2 = 0.19$, df = 49, $F = 11.066$, $P < 0.01$) of those nests which could be potentially affected by avian predators (see Methods). Nests constructed in 1992, however, yielded a stronger relationship between concealment and production where nest concealment explained 38% of the variance ($r^2 = 0.38$, df = 27, F = 15.61, $P < 0.01$). No such relationship was found for nests in 1993 ($r^2 = 0.08$, df = 21, F = 1.653, $P > 0.21$), when overall failure rates were lower (Johnson 1994).

DISCUSSION

If nest site selection is closely tied to fitness, given its effect on fledgling production, then the ability to select well-hidden sites should be

common where visual predators predominate. Decreases in residual reproductive value have been hypothesized as a mechanism for innate age-specific dominance in reproductive effort for older birds. Moreover, if there are age-specific differences in territory acquisition (e.g., Sherry and Holmes 1989, 1990), then the optimal nest sites that are within these selected territories should be used predominately by older birds. Given the predator composition, structural heterogeneity of the understory, and previous failure rates of Wood Thrush nests at UDW (Roth and Johnson 1993, Johnson 1994), it is reasonable to assume that older birds would conceal their nests more than yearlings. I found no evidence that this was true.

The effect of experience has been observed to enhance foraging success (Desrochers 1992) and reproduction in birds (Pyle et al. 1991). Likewise, an age-specific difference in nest concealment seems reasonable if birds learn from previous avian predation events. Qualitative observations of individuals suffering suspected avian predation losses did not consistently result in birds subsequently choosing more greatly concealed sites nor did the data reflect this logic.

Given the evidence (i.e., predator community structure, vegetational heterogeneity, Wood Thrush response to Blue Jays and Common Grackles around nest site (Johnson 1994), witnessed events, and post predation evidence), avian predation may be a strong regulating force on fledgling production of Wood Thrushes at UDW. Westmoreland and Best (1985) attribute 79% of the nest failures to avian predation, and Yahner and Delong (1992) attribute 90% of unsuccessful nests in a Pennsylvania woodlot to avian predators. Additionally, Hoover et al. (1995) attribute most of the Wood Thrush losses to the same suspected avian predators in several Pennsylvania forests. Therefore, there should be a clear overall advantage to concealing nests from visually oriented predators. In 1992, the data reflected this advantage. In 1993, there was no association. However, during this period, failure rates (and therefore predation events) were lower (Johnson 1994). In this light, any clear advantage of nest concealment would not have been apparent.

Nest concealment may be less important where predator communities are different or where vegetational structure selectively permits predator access. The plant species most frequently used by Wood Thrush in UDW is *Viburnum dendatum* (Roth, unpub. data), which cannot easily support the weight of larger mammalian predators present at UDW. In habitats where *Viburnum* or structurally similar understory is not present, mammalian and reptilian predation may be an important factor. These pressures may be variable in time as well as space and be such to offset or modify the selective advantage of concealment. Further, other factors such as

microclimate, food abundance, shrub density, as a host of multiple nest patch factors, may additionally be instrumental in nest site selection (Holway 1991); vegetation density may be only highly correlated with these attributes.

A stronger relationship between male age and concealment might have been found had I quantified the vegetation structure of the nest patch. Previous data from UDW and from other studies have shown older birds to breed in superior habitats more often than yearlings (Sherry and Holmes 1989, 1990, Johnson 1994). Greater concealment may be a circumstance of greater nest patch vegetation than nest site vegetation per se. Greater vegetation in the entire nest area may hold a greater advantage in concealment of adult movements to and from the nest as well as yielding a greater probability of nest concealment from sheer random nest placement within the nest patch. In addition, it must be noted that cryptic nest placement would not be measured in these analyses, as only vegetation actually concealing the nest was measured.

My data suggest that concealment of the nest can be advantageous through lower probability of avian predation. However, the selective advantage of greater nest concealment by experienced birds was not evident in this population of Wood Thrush.

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EFFECTS OF FEMALE COWBIRD REMOVAL ON REPRODUCTIVE SUCCESS OF HOODED WARBLERS

BRIDGET J. M. STUTCHBURY[1]

ABSTRACT.—Female Brown-headed Cowbirds (*Molothrus ater*) were systematically removed from two adjacent Hooded Warbler (*Wilsonia citrina*) breeding populations for 2–5 years. All female cowbirds detected using playbacks were removed. Although an average of only 17 female cowbirds were removed annually from each population, this reduced the frequency of parasitism to < 10% of nests in most years. The average percentage of nests parasitized (53%) in populations with no cowbird control (N = 3) was significantly higher than for populations where female cowbirds were being removed (9%, N = 7). Experimental reduction of parasitism, however, did not result in a significant increase in number of young fledged per nest. Predation of entire clutches and broods effectively swamped the gains achieved by controlling female cowbirds. The effectiveness of cowbird removals as a management tool will likely vary with cowbird abundance and host species, but this study suggests that beneficial effects for the host species can be minimal. *Received 27 Feb. 1996, accepted 20 Aug. 1996.*

The alarming decline of many North American songbird populations over the past few decades (Robbins et al. 1989, Askins et al. 1990) has lead to intensified efforts to identify the causes of this decline (e.g., Hagan and Johnston 1992). There is much debate about whether the critical factor causing the songbird decline is loss of winter habitat (e.g., Robbins et al. 1989) or fragmentation of breeding habitat (e.g., Robinson et al. 1995b, Sherry and Holmes 1996). Brown-headed Cowbirds (*Molothrus ater*) have been implicated in the songbird decline (e.g., Brittingham and Temple 1983, Robinson et al. 1995b) because they are brood parasites of songbirds. Forest fragmentation in eastern North America, combined with an increase in cowbird numbers (Brittingham and Temple 1983), has lead to unusually high rates of brood parasitism on many forest songbirds (e.g., Robinson et al. 1995b).

There have been calls to control cowbird populations on a large scale as a management tool for slowing population declines (Robinson et al. 1995b). However, few studies have actually controlled adult cowbirds and assessed the impact on songbird breeding success. In the most famous example, cowbird control in the Kirtland's Warbler (*Dendroica kitlandii*) breeding area decreased parasitism and increased the average number of young fledged per nest (Kelly and DeCapita 1982, Walkinshaw 1983), but this did not lead to an increase in population numbers (Mayfield 1993). Cowbird control programs for the Least Bell's Vireo (*Vireo belii pusillus*) and Black-capped Vireo (*V. atricapillus*) have also reduced par-

[1] Dept. of Biology, York Univ., North York, Ontario, Canada M3J 1P3.

asitism and increased nesting success (reviewed in Robinson et al. 1995a). Cowbird removals are apparently linked to increasing populations of the Least Bell's Vireo and Willow Flycatcher (*Empidonax traillii extimus*) (reviewed in Robinson et al. 1995a). In this study, I examined the effectiveness of female cowbird removals for increasing the reproductive success of Hooded Warblers (*Wilsonia citrina*), a species that is not threatened and has extensive breeding habitat remaining. The frequency of brood parasitism and nesting success of Hooded Warblers in a cowbird removal area was compared with populations without cowbird control.

METHODS

I conducted this study from 1991–1995 in Crawford County, Pennsylvania (41°N, 79°W), in conjunction with other on-going research (Stutchbury et al. 1994, Neudorf 1996, Tarof 1996, Stutchbury and Evans Ogden 1996). The main study site of 100 ha mixed hardwood forest supports about 40 breeding pairs annually. Another study area (50 ha) continuous with the main study site was included, beginning in 1994, and supported an additional 20 pairs. In 1994 and 1995 we also located breeding Hooded Warblers in several nearby forests (10–30 ha) where no cowbird control was done. Nesting adults were banded with U.S. Fish and Wildlife Service bands and color banded. We found nests at the building, egg-laying, or incubation stage, usually by following the female to the nest. We checked nests every 3–5 days to determine nesting success. All cowbird eggs were removed from nests. Nestlings were banded, and in many cases, blood samples were taken for use in DNA fingerprinting (Stutchbury et al. 1994). Cowbird parasitism frequency in the main study area for the years 1984–90, prior to the cowbird removals, were obtained from studies by E.S. Morton (unpubl. data).

Female cowbirds were removed by shooting from late April through mid-June. From 07:00–11:00 h EST, playbacks of the female "chatter" call were used to lure female cowbirds to the speaker (e.g., Dufty 1982, Yokel 1989). This also attracted male cowbirds. Beginning the first week of May, and about once per week, 3-min playbacks were performed every 100 m along a circuit through the study site. Cowbirds were collected with a shotgun. In most years, a comparable number of male cowbirds (15–20) were also removed because unmated males could potentially attract females to the area. Relatively few males (< 10) were removed in 1995 because the removal of females alone appeared sufficient for reducing parasitism rates.

RESULTS

An average of 17 female cowbirds were removed from each population per year (Table 1). Cowbirds were most abundant in May, and few females were seen or heard after mid-June. Most (56%) female cowbirds were removed during the first two weeks of May, and only a few (16%) were removed in June. Cowbirds were removed throughout the study site, including the locations most distant (500 m) from the forest edge.

Although only 8–30 female cowbirds were removed annually from each population, this likely represented most of the breeding females. Removals on this scale were highly effective in reducing parasitism on Hooded Warbler nests. The frequency of cowbird parasitism in the main

TABLE 1

NUMBER OF MALE AND FEMALE COWBIRDS REMOVED EACH YEAR AND PERCENTAGE OF NESTS PARASITIZED IN EACH HOODED WARBLER POPULATION

Population (# nests)	Cowbirds removed		Parasitism frequency
	Male	Female	
Brown Hill			
1984–1990 (28)	0	0	64%
1991 (45)	9	13	0%
1992 (62)	26	15	13%
1993 (56)	15	29	34%
1994 (40)	29	31	3%
1995 (38)	4	12	5%
Morton Farm			
1994 (22)	12	8	0%
1995 (17)	3	14	6%
Berlin			
1994 (8)	0	0	38%
1995 (24)	0	0	58%

Brown Hill population was 64% (18 of 28 nests) prior to the removals (Table 1). The parasitism frequency was low (0–13%) in the Brown Hill population most years of the removals, except 1993. Parasitism was also very low (< 10%) in the adjacent Morton Farm population in both years of removals (Table 1). The average level of parasitism in populations where female cowbirds were removed (9%, N = 7) was significantly lower (Mann-Whitney *U*-test, $z = 2.39$, $P < 0.05$) than for the populations with no cowbird control (53%, N = 3).

Both clutch size and number of young hatched were significantly higher for nests in areas where parasitism was reduced to ≤ 5% of nests (Table 2). The average number of young fledged from all nests (including those preyed upon) in areas with very low parasitism was not significantly ($t = 0.53$, $P > 0.50$) higher than for populations with high parasitism (Table 2). The number of young fledged per nest did not vary significantly with the percentage of nests parasitized (Fig. 1; $r^2 = 0.16$, $P^2 = 0.28$). Predation frequency varied from 22%–52% among populations, so many nests that escaped parasitism were preyed upon. The frequency of predation did not vary consistently with parasitism frequency ($r^2 = 0.16$, $P = 0.29$).

Predation on entire broods effectively removed the increase in nesting success that would be expected if cowbird parasitism were absent. This

TABLE 2

CLUTCH SIZE, NUMBER HATCHED AND NUMBER FLEDGED FOR HOODED WARBLER NESTS IN POPULATIONS WITH VERY LOW PARASITISM (≤5% NESTS) AND HIGH PARASITISM (>30%)[a]

Variable	All nests		Successful nests	
	Low (N = 145)	High (N = 88)	Low (N = 81)	High (N = 51)
Clutch size	3.60 (0.62)**	3.08 (0.92)	—	—
No. hatched	2.43 (1.62)*	1.74 (2.63)	3.32 (0.88)**	2.57 (1.30)
No. fledged	1.72 (1.75)	1.60 (1.55)	3.20 (0.96)*	2.74 (0.98)

[a] Means (SD) are given for all nests (including those preyed upon), and for successful nests (those that escaped predation). Statistical significance for *t*-tests indicated by asterisks (**$P < 0.001$, *$P < 0.05$).

can be seen by comparing the productivity of only those pairs whose nest was not preyed upon. Hooded Warbler pairs breeding in areas with low parasitism had an average of 3.20 ± 0.96 young per nest, significantly higher than the 2.74 ± 0.98 young for areas with high parasitism (Table 2). As expected, number of young fledged from successful nests was significantly correlated with percentage of nests parasitized (Fig. 1; $r^2 = 0.60$, $P = 0.01$).

To determine if cowbird removal increased average reproductive success compared with Hooded Warbler populations in other parts of the breeding range, nesting data were obtained from other researchers (Arkansas, T. Martin; Ohio, R. Dettmers; Ontario, M. Gartshore). The number of young fledged from these three populations was compared to the Pennsylvania populations where cowbird parasitism was experimentally reduced to ≤

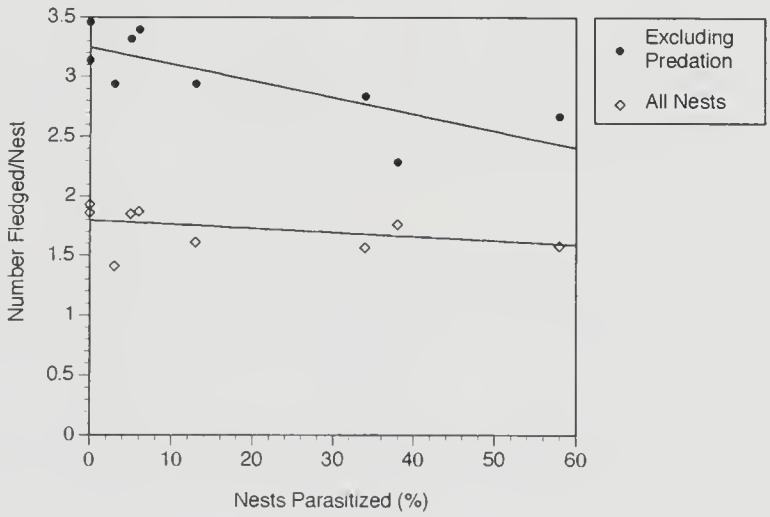

FIG. 1. Mean number of young fledged per nest (for all nests and for only those that escaped predation) for each Hooded Warbler population versus the percentage of nests parasitized.

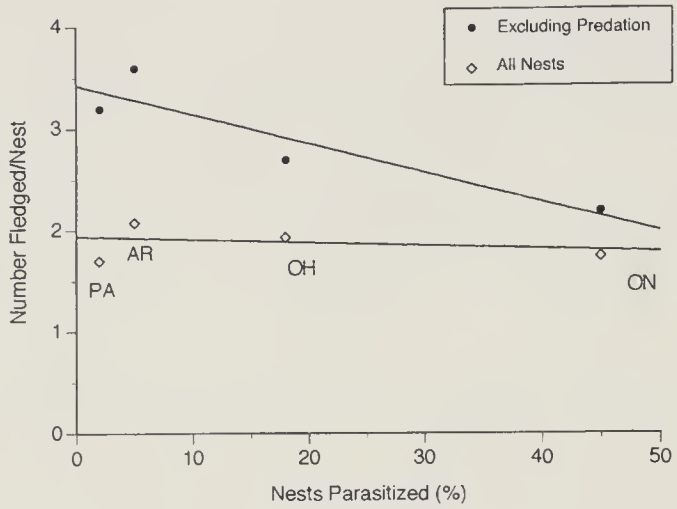

FIG. 2. Mean number of young fledged per nest (for all nests and only those that escaped predation) for the Pennsylvania populations with ≤ 5% parasitism (N = 145 nests) and for populations in Arkansas (N = 99), Ohio (N = 82) and Ontario (N = 28).

5% (Fig. 2). Number of young fledged per nest did not vary with the percentage of nests parasitized. In these studies, predation frequency was highest (48%) for Pennsylvania, modest for Arkansas (39%) and Ohio (30%) and relatively low for Ontario (21%). Reproductive success in the Pennsylvania population where cowbirds were controlled was similar to that of the Arkansas population where parasitism rates are naturally low (Fig. 2). When predation was removed as a factor, the expected correlation between reproductive success and parasitism was clear (Fig. 2).

DISCUSSION

There are two main findings of this cowbird removal experiment. First, removing a small number of female cowbirds each year early in the breeding season dramatically reduced parasitism rates on Hooded Warblers. Second, removal of female cowbirds did not result in a significant increase in reproductive success.

Most cowbird removal experiments have been successful in reducing the frequency of cowbird parasitism (reviewed in Robinson et al. 1995a). The scale of the cowbird removals clearly depends on the size of the breeding area and the density of cowbirds. The Kirtland's Warbler project removed over 1000 female cowbirds per year using drop-in traps located throughout the 4000-ha breeding areas (Walkinshaw 1983). In the present study, playbacks of female cowbird calls were used to attract local females that were likely to parasitize nests within the 150 ha removal site. Although only a modest number of females were removed per population, this apparently represented almost the entire breeding population of cow-

birds. Female cowbirds removed early in the season were replaced by other individuals, so it is difficult to estimate the local density of cowbirds. The maximum estimate of female cowbird density is about 20/km^2 for the Brown Hill and Morton Farm populations, which is at the low end of range reported for cowbirds (Yokel 1989). Whether such small scale cowbird removal would be equally successful in reducing parasitism in regions of high cowbird density is not known. There was no evidence that removals in one year had any carry over effect in terms of reducing cowbird numbers the subsequent year.

Although cowbird removals dramatically increased reproductive success by 0.8–1.9 fledglings per nest in the Kirtland's Warbler (Kelly and DeCapita 1982), Least Bell's Vireo, and Black-capped Vireo (reviewed in Robinson et al. 1995a) this was not the case for Hooded Warblers. Clutch size and number of young hatched were significantly higher for nests in populations with very low parasitism (Table 2), reflecting the low frequency of egg losses due to cowbirds. Number of young fledged, however, was not significantly higher for populations with low parasitism due to the effects of nest predation (Fig. 1, Table 2). Cowbird removal resulted in an average increase of only 0.12 young fledged per Hooded Warbler nest. To put this into perspective, this amounts to about five extra fledglings produced from a population of 40 breeding pairs of Hooded Warblers.

When compared with several Hooded Warbler populations across the breeding range (Fig. 2), cowbird parasitism was not significantly related to number of young fledged per nest. Variability in predation frequency among populations tended to overshadow small differences in reproductive success that resulted from cowbird parasitism. These results suggest that cowbird removals on a large scale to reduce parasitism may not result in any significant increase in productivity of Hooded Warblers. Cowbird removal may have minimal advantages in other species too, because predation often causes much higher daily mortality on nests than does parasitism (Donovan et al. 1995).

Cowbird removals may be more likely to benefit host species in areas with extreme forest fragmentation and many cowbird eggs per host nest (e.g., Robinson et al. 1995a). Also, some species fledge few of their own young when parasitized (e.g., Walkinshaw 1983), so cowbird parasitism can outweigh predation as a leading cause of nest mortality. Clearly, removal of cowbirds in specific populations of endangered and threatened species can increase reproductive success of particular host species (Walkinshaw 1983, Robinson et al. 1995a). Small scale removals of cowbirds in specific research areas can also be valuable for studying the behavior and ecology of songbirds in the absence of parasitism. Studies of the

evolution of parental care, fledgling care, and extra-pair mating tactics in eastern forest songbirds (e.g., Stutchbury et al. 1994, Neudorf 1996, Stutchbury and Evans Ogden 1996, Tarof 1996) are hampered by unnaturally high levels (40–60%) of brood parasitism. The effectiveness of cowbird removals as a management tool will likely vary with cowbird abundance and host species, but this study indicates that beneficial effects for the host species can be minimal.

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EFFECTS OF PRESCRIBED FIRE ON MOVEMENTS OF FEMALE SAGE GROUSE FROM BREEDING TO SUMMER RANGES

RICHARD A. FISCHER[1], WAYNE L. WAKKINEN[2], KERRY P. REESE[1], AND JOHN W. CONNELLY[3]

ABSTRACT.—We compared summer movement patterns of female Sage Grouse (*Centrocercus urophasianus*) in southeastern Idaho before (1987–1989) and after (1990–1992) a prescribed fire which removed vegetation cover, primarily Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), from approximately 57% of a 5800 ha area. Grouse moved 1–69 km ($\bar{x}$ = 17.8 ± 2.0 km [SE]; N = 81) from breeding and nesting areas to summer ranges, predominantly in northwest or southwest directions during the 6-year period. There was no difference in timing, distance, or direction moved between birds captured in burned and unburned habitats. The data provided further evidence of traditional migration routes for Sage Grouse breeding and nesting in the Big Desert. *Received 16 Mar. 1996, accepted 1 Sept. 1996.*

Several species of Tetraoninae are migratory (Hoffman and Braun 1975, Herzog and Keppie 1980, Cade and Hoffman 1993, Schroeder and Braun 1993). Some Sage Grouse (*Centrocercus urophasianus*) populations are migratory when year-round habitat requirements cannot be met in proximal areas. Thus, some grouse seek suitable habitat in more than two seasonal-use areas that are often widely separated. Interseasonal movements of 20–81 km have been documented for Sage Grouse populations (Connelly and Markham 1983, Gates 1983, Berry and Eng 1985, Wakkinen 1990). The Big Desert sagebrush ecosystem in southeastern Idaho provides important Sage Grouse breeding, nesting, and brood-rearing habitat (Connelly et al. 1988, Wakkinen 1990). However, during dry summers, vegetation food sources become desiccated, and Sage Grouse migrate to more mesic summering areas (Connelly et al. 1988, Fischer et al. 1996). Grouse return to breeding range beginning in late fall, presumably to be near leks for the onset of breeding the following spring (Robertson 1991, Connelly et al. 1988).

Berry and Eng (1985) and Connelly et al. (1988) noted the importance of identifying Sage Grouse seasonal use areas and migration routes between or among these areas. Their research suggested that migratory Sage Grouse populations should be defined on a temporal and geographic basis

[1] Dept. of Fish and Wildlife Resources, Univ. of Idaho, Moscow, Idaho 83843 (Present address RAF: U.S. Army Corps of Engineers, Waterways Experiment Station, Environmental Laboratory, 3909 Halls Ferry Rd., Vicksburg, Mississippi 39180-6199).
[2] Idaho Dept. of Fish and Game, HCR 85 Box 323-J, Bonners Ferry, Idaho 83805.
[3] Idaho Dept. Fish and Game, 1345 Barton Rd., Pocatello, Idaho 83204.

and that all seasonal habitats and migration corridors should be managed accordingly. Habitat manipulation, such as sagebrush removal, has contributed to declining populations of Sage Grouse throughout their range (Autenrieth 1969, Klebenow 1970, Swenson et al. 1987, Braun 1995). Controlled burning has become an increasingly popular method of sagebrush removal on western rangelands (Frandsen 1985, Bunting et al. 1987). The influence of fire on Sage Grouse winter movements (Robertson 1991), breeding males (Benson et al. 1991), and brooding females and brood habitat (Martin 1990, Fischer et al. 1996) has been investigated, but little is known about the influence of fire on migration patterns (e.g., timing, use of traditional routes) during spring and summer. Sage Grouse returning to traditional leks (Dunn and Braun 1985) and specific nesting areas (Fischer et al. 1993) may find altered habitats unsuitable for breeding and/or nesting and, therefore, initiate migration earlier than individuals in unaltered habitats. Our objectives were to document direction and distance of summer movements and to identify summer ranges used by migrating female Sage Grouse. We tested the hypotheses that (1) Sage Grouse show no directional trend when moving from breeding and nesting ranges to summer ranges, and that (2) there are no differences in direction, timing, or distance of movement between breeding and nesting range and summer ranges, after prescribed fire for female Sage Grouse captured in unburned habitat and in or immediately adjacent to burned habitat.

STUDY AREA AND METHODS

We studied Sage Grouse from 1987 through 1992 on a 20,000-ha portion of the 240,867-ha Big Desert in Blaine and Butte counties on the Upper Snake River Plain, southeastern Idaho (43°24′N, 113°07′W). The topography varies from flat to gently undulating terrain with an interspersion of exposed silicic and basaltic volcanic outcrops and craters. Elevations ranged from 1536 m to 2304 m. Median precipitation during the study was 17.1 cm, which was below the long-term median of 24.0 cm (1956–89; data from Agric. Engineering Dept., Univ. Idaho). Hironaka et al. (1983) classified the Big Desert as a Wyoming big sagebrush/bluebunch wheatgrass (*Agropyron spicatum*) habitat type; threetip sagebrush (*A. tripartita*), rabbitbrush (*Chrysothamnus* spp.), Sandberg bluegrass (*Poa sandbergii*), and bottlebrush squirreltail (*Sitanion hystrix*) were abundant. As part of a larger study to investigate differences in ecology of Sage Grouse before and after fire (Fischer 1994), the Bureau of Land Management prescribed burned a 5800 ha portion of the northern half of the study area during late summer 1989. All portions of the study area were grazed by cattle, except for the burned area, which was ungrazed for one year prior to and two years following the burn. Wakkinen (1990) and Fischer (1994) provided detailed descriptions of the Big Desert study area.

Data collection.—Sage Grouse were captured by spotlighting at night (Giesen et al. 1982, Wakkinen et al. 1992) on and near leks during March and April 1987–1992. We captured 219 females and fitted them with solar- or battery-powered, poncho-mounted (Amstrup 1980) transmitters. The transmitter and poncho weighed approximately 20 g, which was ≤2% of female body weights. We classified females as either treatment or control based

upon whether they were captured on leks in (N = 5) or within one km (N = 7) of the burn or ≥3.5 km south of the burn (N = 18), respectively. Females on leks within one km of the burn were considered treatment females because fire removed potential nesting habitat for these birds (females on the study area moved 3.4 ± 0.4 km [SE] from lek-of-capture to nest [Fischer 1994]). The distance of the next closest active lek to the burn was 3.5 km, and none of the females from this or any other control lek nested within the burn.

We used radiotelemetry to identify timing, distance, and direction of movements to summer ranges. Following the breeding and nesting seasons, we attempted to locate radiomarked grouse at least once every two weeks using ground and aerial searches. However, because the birds occupied an area over 4000 km^2 during summer, it was not possible to search thoroughly all potential summer ranges during each flight. Thus, we did not locate all radiomarked birds every two weeks. Due to the wide distribution of birds, 46% of locations after 15 June were from fixed-wing aircraft, compared to 26% prior to 15 June. Median error for aerial locations of six transmitters placed at fixed locations was 294.9 m. We plotted each location on 7.5-min topographic maps using the Universal Transverse Mercator grid system. Location data were partitioned into two-week intervals starting on 1 May and continuing through 30 July. The final interval included all locations between 1 August and 30 September, because of smaller sample sizes due to a reduction in flight frequency after birds had moved to summer ranges. Within intervals, we assigned each location to appropriate 90° quadrants (Northeast Q-I = 0–90°; Southeast Q-II = 90–180°; Southwest Q-III = 180-270°; Northwest Q-IV = 270–360°). Quadrants were centered on the lek-of-capture for non-nesting females or females whose nesting attempts could not be identified (see Connelly et al. 1993), whereas the nest was used as the point-of-origin for nesting females.

We calculated straight-line distance from the point of origin to all subsequent locations of each female during and after the nesting season. We arbitrarily decided that migration was initiated when a female had moved ≥5 km from her respective point of origin because mean lek-to-nest distance for female Sage Grouse in the study area was 3.44 km (Fischer 1994) and 76% of females nested within 5 km of lek of capture. Within each time interval, we calculated the farthest distance moved from point-of-origin for each individual and percentage of birds that were ≥5 km from point of origin. Because the number of radio locations after 1 August was limited, the last distance recorded for all individuals located after 15 June represented the minimum straight-line distance of summer movements.

Data analysis.—We separated data into preburn (1987–1989) and postburn (1990–1992) periods and used separate Chi-square tests (Zar 1984) on each data set (treatment and control pooled) to test for homogeneity of locations among the four quadrants within each time interval. Preburn data were then partitioned into females captured on treatment or control leks, and the two data sets were analyzed separately with Chi-square tests to identify any differences in direction of migration from the two areas prior to the fire. Postburn treatment and control data were analyzed in the same manner. We then pooled all data (1987–1992) to investigate whether fire influenced summer migration patterns of females captured on treatment leks, and used a Cochran-Mantel-Haentzel (CMH) statistic (SAS 1988) on the following four variables: Q (Quadrants I-IV), I (2-week time intervals; 1–7), P (before fire, after fire), and Area (treatment, control). The CMH statistic, an *n*-way cross-tabulation contingency table, tested the relationship between counts of treatment and control females in quadrants before and after fire, after adjusting for the possible confounding effects of I and Q (SAS 1988).

We used analysis of variance (ANOVA) on ranks (Conover and Iman 1981) of postburn intervals (1–7) to examine if grouse from treatment and control areas initiated migration at the same time. We also used ANOVA on log-transformed migration distances recorded after

15 June 1990–1992 to detect differences in distances moved by females from treatment and control leks.

RESULTS

We captured 112 females (51 preburn; 61 postburn) on treatment leks and 107 females (47 preburn; 60 postburn) on control leks. Preburn data indicated no differences in quadrant use until July, when grouse moved southwest more frequently than expected. Postburn data indicated grouse moved northwest and southwest proportionately more than expected after June (Table 1). When preburn treatment and control data were analyzed separately, control females moved southwest (Table 2) and treatment females moved southwest and northwest more than expected after June (Table 3). The postburn control and treatment data also indicated more birds moved in southwest and northwest directions (Tables 2 and 3). When all six years of data were pooled, there was a significant Area × P interaction (CMH General Association test statistic = 9.672, P = 0.002), suggesting a potential difference in movement patterns of females captured in treatment and control areas before and after fire.

Timing of postburn movements to summer range was similar for females captured in burned and unburned habitat ($F_{1,106}$ = 0.56, P = 0.456). Mean movements of females from point of origin located after 15 June ranged from 0.2 to 69.3 km ($\bar{x}$ = 17.8 ± 2.0 km [SE]; N = 81). There was no difference in distances moved by females from treatment ($\bar{x}$ = 15.2 ± 2.8 km; N = 36) and control leks ($\bar{x}$ = 19.9 ± 2.7 km; N = 45) ($F_{1,80}$ = 0.05, P = 0.820) or among years ($F_{2,80}$ = 0.02, P = 0.980).

DISCUSSION

Sage Grouse populations are migratory or nonmigratory, depending on plant moisture conditions, vegetal cover, and elevation (Dalke et al. 1960, Beck 1975, Wallestad 1975, Connelly 1982, Fischer et al., in press). Connelly et al. (1988) investigated spring and summer movements of migratory Sage Grouse in southeastern Idaho and found that birds moved as far as 82 km, usually as directional movements from breeding and nesting areas to summer ranges. Sage Grouse on our study area used contiguous areas for wintering, breeding, and nesting, but migrated as far as 69 km to summer ranges. This study and that of Robertson (1991) documented seasonal habitats and migration routes for Big Desert Sage Grouse, which is critical information for managing a migratory Sage Grouse population (Berry and Eng 1985, Connelly et al. 1988). We demonstrated that Sage Grouse in the Big Desert primarily migrated northwest to higher elevations near Arco, Idaho (Q-IV), or southwest to lower elevations near Minidoka, Idaho (Q-III). Connelly et al. (1988) captured Sage Grouse

TABLE 1

FREQUENCY OF OCCURRENCE OF FEMALE SAGE GROUSE IN QUADRANTS CENTERED ON POINT-OF-ORIGIN, PREBURN (1987–1989), AND POSTBURN (1990–1992), BIG DESERT, SOUTHEASTERN IDAHO

	Preburn						Postburn					
		Frequency of occurrence[a]						Frequency of occurrence				
	N[b]	Q-I	Q-II	Q-III	Q-IV	P H_0: Homogeneity	N	Q-I	Q-II	Q-III	Q-IV	P H_0: Homogeneity
01–15 May	75	0.40	0.23	0.15	0.23	0.082	93	0.31	0.23	0.19	0.27	0.420
16–31 May	79	0.28	0.25	0.17	0.30	0.124	57	0.35	0.14	0.21	0.30	0.120
01–14 Jun	63	0.32	0.25	0.19	0.29	0.572	43	0.21	0.19	0.28	0.33	0.560
15–30 Jun	53	0.26	0.21	0.21	0.32	0.568	71	0.24	0.27	0.27	0.23	0.940
01–15 Jul	66	0.12	0.23	0.47	0.24	0.001	31	0.10	0.19	0.58	0.13	0.000
16–31 Jul	52	0.06	0.19	0.52	0.23	0.000	24	0.33	0.00	0.25	0.42	0.025
01 Aug–30 Sep	82	0.02	0.15	0.57	0.26	0.000	14	0.00	0.14	0.36	0.50	0.040

[a] Q-I = 0–90°; Q-II = 90–180°; Q-III = 180–270°; Q-IV = 270–360°.
[b] Number of female Sage Grouse located during each time interval over a 3-year period.

TABLE 2

FREQUENCY OF OCCURRENCE OF FEMALE SAGE GROUSE IN QUADRANTS CENTERED ON POINT-OF-ORIGIN PREBURN (1987–1989), AND POSTBURN (1990–1992) CONTROL AREA, BIG DESERT, SOUTHEASTERN IDAHO

	Preburn						Postburn					
		Frequency of occurrence[a]						Frequency of occurrence				
	N[b]	Q-I	Q-II	Q-III	Q-IV	*P* H_0: Homogeneity	N	Q-I	Q-II	Q-III	Q-IV	*P* H_0: Homogeneity
01–15 May	37	0.41	0.27	0.16	0.16	0.123	53	0.32	0.17	0.23	0.28	0.430
16–31 May	37	0.32	0.35	0.11	0.22	0.141	28	0.39	0.07	0.14	0.39	0.030
01–14 Jun	31	0.39	0.26	0.13	0.23	0.240	25	0.24	0.08	0.32	0.36	0.220
15–30 Jun	25	0.32	0.32	0.12	0.24	0.455	44	0.21	0.23	0.34	0.23	0.580
01–15 Jul	28	0.22	0.29	0.39	0.11	0.220	22	0.05	0.18	0.64	0.14	0.000
16–31 Jul	20	0.10	0.30	0.50	0.10	0.034	10	0.50	0.00	0.20	0.30	0.174
01 Aug–30 Sep	31	0.03	0.26	0.68	0.03	0.000	7	0.00	0.14	0.57	0.29	0.187

[a] Q-I = 0–90°; Q-II = 90–180°; Q-III = 180–270°; Q-IV = 270–360°.
[b] Number of female Sage Grouse located during each time interval over a 3-year period.

TABLE 3

FREQUENCY OF OCCURRENCE OF FEMALE SAGE GROUSE IN QUADRANTS CENTERED ON POINT-OF-ORIGIN, PREBURN (1987–1989), AND POSTBURN (1990–1992) TREATMENT AREA, BIG DESERT, SOUTHEASTERN IDAHO

	Preburn						Postburn					
		Frequency of occurrence[a]						Frequency of occurrence				
	N[b]	Q-I	Q-II	Q-III	Q-IV	*P* H_0: Homogeneity	N	Q-I	Q-II	Q-III	Q-IV	*P* H_0: Homogeneity
01–15 May	38	0.40	0.18	0.13	0.29	0.250	40	0.30	0.30	0.15	0.25	0.490
16–31 May	42	0.24	0.17	0.21	0.38	0.240	29	0.31	0.21	0.28	0.25	0.820
01–14 Jun	32	0.25	0.25	0.25	0.25	0.999	18	0.17	0.33	0.22	0.28	0.770
15–30 Jun	29	0.21	0.14	0.28	0.38	0.310	27	0.30	0.33	0.15	0.22	0.560
01–15 Jul	42	0.05	0.17	0.48	0.31	0.000	9	0.22	0.22	0.44	0.12	0.562
16–31 Jul	32	0.03	0.13	0.53	0.31	0.000	14	0.21	0.00	0.29	0.50	0.072
01 Aug–30 Sep	51	0.02	0.08	0.51	0.39	0.000	7	0.00	0.14	0.14	0.71	0.040

[a] Q-I = 0–90°; Q-II = 90–180°; Q-III = 180–270°; Q-IV = 270–360°.
[b] Number of female Sage Grouse located during each time interval over a 3-year period.

adjacent to our study area that moved to summering areas on irrigated lawns or agricultural fields. Females in our study that moved northwest summered in or near agricultural fields or moved beyond agriculture to natural summer ranges (i.e., mesic mountain valleys). Grouse moving southwest were found primarily in or near agricultural fields but also in mesic meadows near these fields. Traditional migration routes in this direction probably were to the higher foothills and mountain meadows located farther to the west. Similar to Connelly et al.'s (1988) findings, many birds that encounter agriculture remain in or near these fields during summer. Most irrigated agricultural areas now used by Sage Grouse as summer habitats provide abundant lush vegetation where none previously existed. These areas were historically xeric sagebrush habitats that probably were not suitable summer range. However, the effects on females of stopping short of traditional summer ranges to use agricultural areas is unknown. Our findings were consistent with those of Connelly et al. (1988) who concluded that most grouse in the Big Desert use traditional migration routes. To support this contention, grouse on our study area could have moved northeast 15–20 km to irrigated agricultural fields, but significantly fewer grouse than expected moved to these areas during summer.

The hypothesis that fire has no influence on Sage Grouse migration was statistically rejected. The significant Area x P interaction suggested that movements of birds from burned and unburned areas differed before and after fire. However, the main differences in observed movement patterns of females between areas was the higher frequency of postburn females from the control moving northwest and the lower frequency of postburn females from the treatment moving southwest (Q-III). Assigning this statistical difference to a treatment effect is dubious and may be related to sampling effort among quadrants. More extreme departures from preburn migrational patterns, especially for treatment females, would have provided a stronger case for true differences before and after fire. The same migration routes were consistently used disproportionately both pre- and postburn, again providing evidence for the traditional nature of these routes. Because grouse moved up to 69 km from breeding or nesting range to summer range, the burned area within breeding/nesting range represented only a small fraction of the annual range of females captured in the treated area. Habitat fragmentation, resulting from removal of large blocks of sagebrush along traditional migration routes, or in summer range, may influence migratory patterns or distribution of Sage Grouse.

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REGULATION OF GROWTH IN RED KITES AND IMPERIAL EAGLES

JAVIER VIÑUELA[1] AND MIGUEL FERRER[2]

ABSTRACT.—We analyzed variability in growth of Red Kite (*Milvus milvus*) chicks using biometrical measures and urea and alkaline phosphatase blood levels. We used variables estimating relative mass and tarsus length growth rates during the 5–7 days before every blood extraction (short-term growth) and deviations of size (mass and tarsus length) from population averages at the age of blood extraction (long-term growth). We found a significant relationship between blood levels of alkaline phosphatase and short-term tarsus growth rate but not with long-term tarsus growth. Urea levels were correlated with long-term mass growth but not with short-term growth. We found some chicks with relatively rapid mass growth, slow tarsus growth, and low levels of alkaline phosphatase after periods of fasting. Chicks of Imperial Eagles (*Aquila adalberti*) showed less variable nestling periods but higher and more variable blood urea levels. These differences agree with theoretical predictions about the evolution of growth regulation abilities in relation to feeding ecology: the species with a more variable growth and more resistence to food deprivation can experience a more irregular and unpredictable food supply. *Received 4 Dec. 1995, accepted 10 April 1996.*

Two hypotheses have been proposed to explain patterns of growth in birds. Ricklefs (1968) proposed that chicks grow at the maximal rate allowed by food intake. Physiological or cellular constraints would determine theoretical maximum growth rate (Maximization Hypothesis). Case (1978) criticized this hypothesis, arguing that rapid growth could be associated with higher mortality rates and proposed that growth rates could be adapted to the ecological features of species (optimization hypothesis; also see O'Connor 1978). These are not mutually exclusive hypotheses, but their relative importance could vary between species depending on ecological constraints (Ricklefs 1984). The optimization hypothesis assumes that growth rates may be maintained below a given level by active control (Callow and Townsend 1981) and predicts that the degree of variability and control of growth rates depends mainly on the predictability and stability of food resources during the nestling period (O'Connor 1978). It is well known that growth rates can be affected by a large variety of environmental factors (Ricklefs 1983). In species with a small clutch size and unpredictable food resources at the time of laying, variable growth rates may work as a fine-tuning mechanism to regulate productivity (O'Connor 1984, Donázar and Ceballos 1989, Veiga and Hiraldo 1990).

Although growth in birds has been extensively studied by biometrical

[1] Museo Nacional de Ciencias Naturales, CSIC, José Gutierrez Abascal 2, 28006-Madrid, Spain.
[2] Estación Biológica de Doñana, CSIC, Avda. Maria Luisa s/n, 41013-Sevilla, Spain.

and observational procedures, experimental and physiological studies are relatively less common (Ricklefs 1983), and hematological indices have rarely been applied to the study of patterns of growth of wild birds (but see Cherel et al. 1987).

In this paper we analyze growth variability in the Red Kite (*Milvus milvus*), using biometrical and physiological methodologies, and we explore the possible existence of mechanisms to regulate growth rate. We compare variables between Red Kites and Spanish Imperial Eagles (*Aquila adalberti*). The Red Kite is an opportunistic predator (Delibes and García 1984, Sunyer and Viñuela 1994), while the Imperial Eagle is considered a highly specialized predator of rabbits, an abundant and predictable prey across its range (González 1989, Ferrer 1994). Models based on the optimization hypothesis predict that the species with a more irregular and unpredictable food supply should exhibit a more flexible growth (O'Connor 1978). Thus, growth rates should be more variable in Red Kites than in Imperial Eagles.

METHODS

We performed this study at Doñana National Park (SW Spain, 37°N 6°5′W) in 1987 and 1988. We measured 44 Red Kite chicks from 26 nests (12 one-chick, 8 two-chick and six three-chick broods). Most nests were visited daily during hatching, so the ages of the chicks were known within an accuracy of one day. In three cases, we estimated age using a linear regression for growth of the seventh primary, a reliable method for aging raptors (e.g., Juillard 1979, Bortolotti 1984, Viñuela and Bustamante 1992). After hatching, nests were visited every 4–7 days (mostly every 5 days). For every visit and chick we recorded (1) tarsus length from the junction with the central toe to the center of tibio-tarsal joint, measured with Vernier caliper to the nearest 0.1 mm, (2) seventh primary length (sheath plus emerged vane to the nearest mm), and (3) mass, measured with Pesola balances (100, 500 or 1000 g, depending on the size of the chick) to the nearest g.

We collected 40 blood samples from chicks aged 28–54 days by extracting 1–2 cc from the brachial vein (see Viñuela et al. 1991). Blood extractions were made at the same time of day to eliminate possible diurnal fluctuations caused by the circadian rhythm (e.g., García-Rodríguez et al. 1987a, Ferrer et al. 1994). The blood was kept cold in heparin-lithium tubes. Centrifuging and separation of plasma (10 min at 3000 G) was completed within 24 hours of extraction, and the sample was kept at 4° C until it was analyzed. Chemical analyses were made in an automatic analyser (Hitachi 705) at the Valme Hospital (Sevilla, Spain). We determined the blood levels of (1) alkaline phosphatase, an enzyme that is intimately linked to ossification and growth of the skeleton (e.g., Fleisch and Newman 1961, Krabbe and Christiansen 1984, Salo et al. 1986, Kan and Cress 1987, Viñuela et al. 1991) and (2) urea, a good indicator of protein catabolism associated with fasting conditions (Sturkie 1976, García-Rodríguez et al. 1987b, Ferrer, 1993). Levels of alkaline phosphatase show significant variation associated with the age of the chicks (Viñuela et al. 1991). To avoid the possible confounding effects induced by this relationship, we used the residuals from the regression of alkaline phosphatase levels and chick age (relatively high or low alkaline phosphatase levels for a given age). Urea levels were not significantly affected by age ($r = -0.19$, $P = 0.24$, $N = 40$).

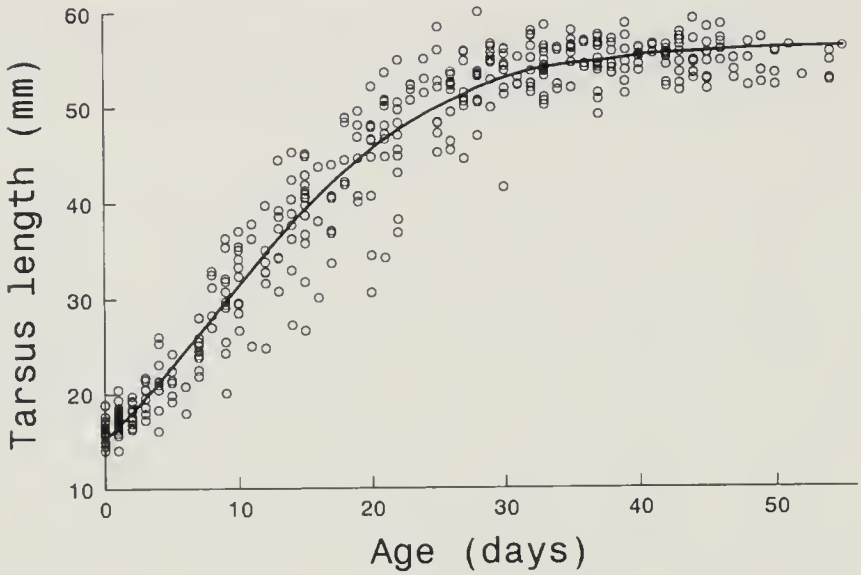

FIG. 1. Tarsus length growth of chicks of Red Kites. Logistic curve shown.

Growth of birds is usually described by means of one of three sigmoid models: the logistic, Von Bertalanffy, or Gompertz equations (O'Connor 1984). The Richards curve may be a more valuable technique, since it is a flexible-shaped model that may explain higher percentages of variance and produce less biased estimates of growth parameters (White and Brisbin 1980, Brisbin et al. 1987, Leberg et al. 1993), but its use in the study of growth of birds has been strongly criticized (Zach 1988). Fixed-shaped growth curves fitting requires the estimation of three growth parameters, while the Richards curve requires four. Consequently, the fixed-shaped models require fewer data for meaningful fitting and are less demanding in terms of data precision (Zach 1988). This has precluded the use of the Richards curve in the study of growth of raptors, where the use of fixed-shaped models is the rule (see e.g., Donázar and Ceballos 1989, Steidl and Griffin 1991, Wiebe and Bortolotti 1994). However, Leberg et al. (1993) presented a form of the Richards curve requiring the estimation of only three parameters, whenever a good estimate of initial size is provided. We have estimated initial size of tarsus from the sample of chicks measured on the day of hatching ($\bar{x} \pm SD = 16.2 \pm 1.4$, $N = 31$). We fitted tarsus growth data from all fledged chicks (Fig. 1) to logistic, von Bertalanffy, Gompertz, and Richards models by means of a non-linear least-squares regression routine (Veiga and Hiraldo 1990, Steidl and Griffin 1991). The logistic curve provided the best fitting, as indicated by the residual mean square error (Steidl and Griffin 1991), it explained a high percentage of the variance (high R^2, Veiga and Hiraldo 1990), and it provided the more realistic growth parameters (Table 1, Fig. 1). Gompertz model did not converge satisfactorily, while von Bertalanffy and Richards models had a lower R^2 and more unrealistic estimates of growth parameters (Table 1). This result confirms those previously reached by Veiga and Hiraldo (1990) who found that growth data of more than 75% of chicks of Red Kites fitted to logistic curves. Zach et al. (1984) also found that Richards model failed to explain a significantly larger proportion of the variance than fixed-shaped models.

Because there usually exists a period of mass recession just before fledging (Hiraldo et al. 1990), and many of the blood extractions were made at this stage of mass recession, we fit mass data with a polynomial curve (Konarzewski and Taylor 1989) (Fig. 1). We included in this curve only the data from chicks 28–54 days old, which encompassed part of the lineal growth stage and final mass recession (when the blood samples were taken).

TABLE 1

TARSUS LENGTH GROWTH PARAMETERS AND NON-LINEAR REGRESSION STATISTICS FOR LOGISTIC (L), GOMPERTZ (G), VON BERTALANFFY (VB), AND RICHARDS (R) CURVES

	L	G	VB	R[a]
Asymptotic tarsus	56	55	58.1	59.9
Growth rate	0.12	0.085	0.08	—
Initial tarsus (b)	15.2	27.5	0.79	—
Growth period (T)[b]	—	—	—	35
Residual sum of squares	4547.3	726,437.6	5078.3	5540
R^2	0.947	−7.49	0.94	0.935

[a] Shape parameter m of Richards curve equal to 0.07, initial size estimated as the average of chicks measured on the day of hatching (16.2).

[b] Constant T of Richards curve is an estimate of the approximate length of the growth period.

To get values independent of the age of chicks to be used as estimates of short- and long-term growth condition, we computed the following variables: (1) long-term mass growth condition (LTMC), the difference between chick mass on the day of blood extraction and the value predicted at that age from the polynomial regression of mass on age; (2) short-term mass growth condition (STMC), the difference between the mass gained by the chick since the previous visit to the nest (4–7 days before) and the average increase predicted by the polinomial regression of mass on age for that age period; (3) long-term tarsus growth condition (LTTC), the difference between tarsus length on the day of blood extraction and tarsus length predicted by the logistic curve; and (4) short-term tarsus growth condition (STTC), the difference between the growth in tarsus length since the previous visit and the growth predicted by the logistic curve.

We present data on urea levels and the duration of the nestling period for 40 chicks of the population of Spanish Imperial Eagles, recorded in the same study area and for chicks with an age equivalent to that of the chicks of Red Kites sampled (half through end of the nestling period). We followed the same methodology described above but, given the endangered status of Imperial Eagles, nests were visited less frequently so growth data are not available. We define the nestling period as the time that elapsed between hatching and first flight of the chicks (Viñuela and Bustamante 1992). The duration of the nestling period was determined for 35 and 30 chicks of Red Kites and Imperial Eagles, respectively.

Statistical analyses were performed on SPSS. We used quadratic equations when suggested by scatter plots. Quadratic curve fitting was done, using multiple regression analyses including the dependent variable and its square power, and using the conditional sum of squares to assess whether the inclusion of the square power significantly increased the variance explained by the model. When indicated by non-significant t-tests, the constant was excluded from the model. To compare the variability of urea levels and the duration of the nestling period among the two species, we used the coefficients of variation and *F*-tests, following the method outlined by Lewontin (1966). Alkaline phosphatase was used as dependent or independent variable depending on the predictions of every analysis (Fig. 2). We predicted that blood levels of alkaline phosphatase could affect growth rate of skeletal structures, so in this case it was considered as independent variable. On the contrary, we predicted that its blood levels could be affected by nutritional condition, as indicated by relative mass growth rate, so in this case it has been considered as dependent variable.

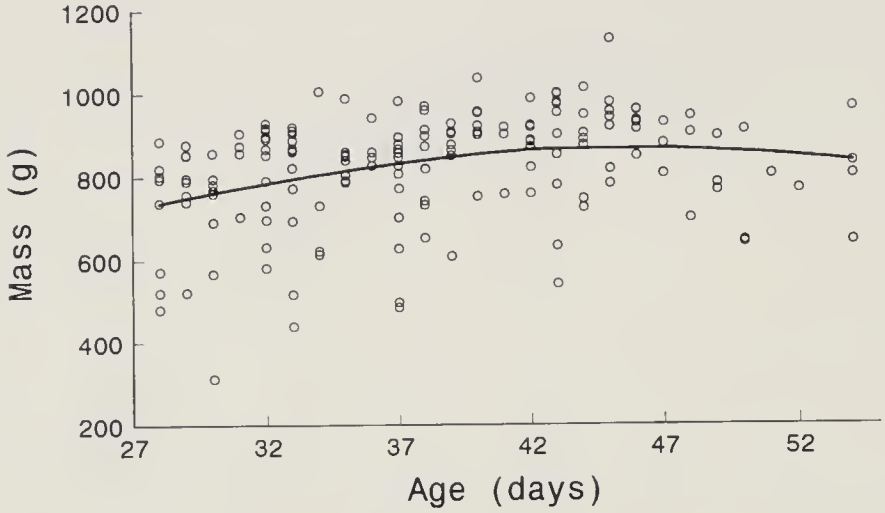

FIG. 2. Mass growth of chicks of Red Kites 28–54 days old (curve shown: $y = 38x - 26.6x^2$, $F = 3957.1$, $P < 0.001$).

RESULTS

We found no significant relationship in Red Kites between long-term tarsus growth (LTTC) or long-term mass growth (LTMC) and relative blood levels of alkaline phosphatase (RAP) ($r = -0.11$, N = 40, $P = 0.48$ and $r = -0.08$, N = 40, $P = 0.63$, respectively) (Fig. 3). Short-term tarsus growth (STTC) and RAP were correlated significantly (Fig. 3). We found a significant quadratic regression between short-term mass growth condition (STMC) and RAP (Fig. 3). The chicks with the highest and the lowest relative mass increases, respectively showed relatively low levels of alkaline phosphatase. We also found a significant quadratic relationship between STTC and STMC (Fig. 4). Relatively low tarsus length increases were associated with the least and the greatest mass increases. Urea levels were negatively correlated with LTMC ($F = 4.5$, $r = -0.32$, N = 40, $P = 0.04$) but not with STMC ($r = -0.12$, N = 40, $P = 0.45$).

Urea levels of chicks of Imperial Eagles were higher and more variable than those of Red Kites (Means: 23.37 mg/dl vs 14.85 mg/dl, $t = 2.36$, $P < 0.05$; coefficients of variation: 97.5% vs 55%, $F = 3.17$, df = 39, 39, $P < 0.01$). The length of the nestling period was more variable in Red Kites (55.5 ± 5.9 days N = 35) than in Imperial Eagles (75.7 ± 4.1 days, N = 30) (coefficients of variation: 10.63% vs 5.48%, $F = 3.76$, df = 34,29, $P < 0.01$).

DISCUSSION

We found a relationship between short term tarsus growth and blood levels of alkaline phosphatase. This result was expected, given the im-

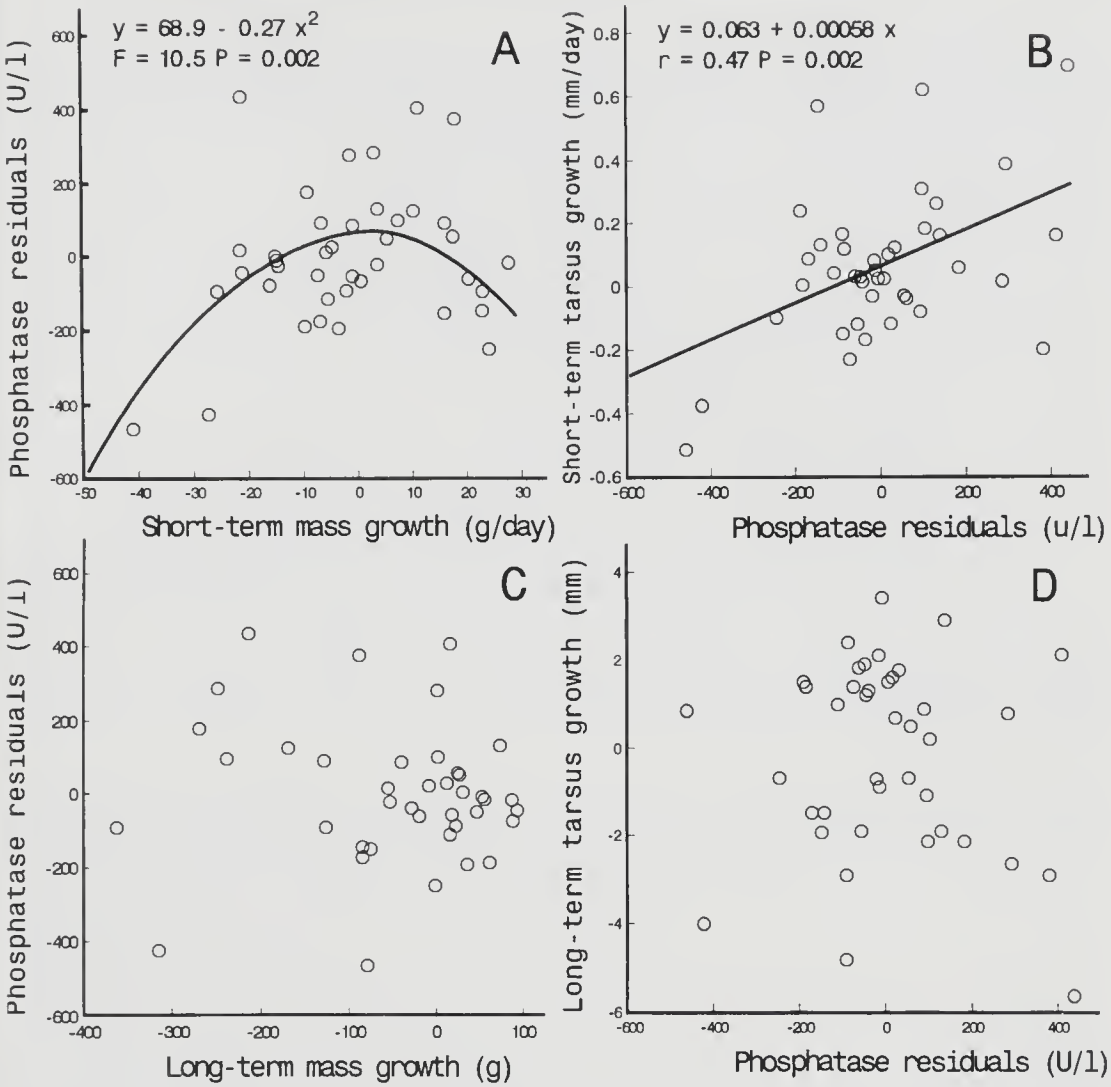

FIG. 3. Plots of short-term mass (A) and short-term tarsus length (B), growth condition variables indicating if the growth during the days before blood extraction was relatively rapid or slow; long-term mass (C) and long-term tarsus length (D) growth condition, indicating if the size on the day of blood extraction was relatively large or small and as dependent (mass plots) or independent variable (tarsus plots) (see Methods), the relative blood levels of alkaline phosphatase (RAP, U/l). No significant relationships were found between RAP and long-term growth variables. See Methods for detailed definitions of the variables.

portant role played by this enzyme in the growth and mineralization of skeletal structures (Krabbe and Christiansen 1984, Kan and Cress 1987, Salo et al. 1986). However, levels of alkaline phosphatase were not correlated with variables indicating long-term growth condition. This suggests that changes in blood levels of this enzyme and the associated growth rate may be rapid responses to food availability. We found some chicks showing relatively high mass growth but slow tarsus growth and relatively low levels of alkaline phosphatase. This situation must corre-

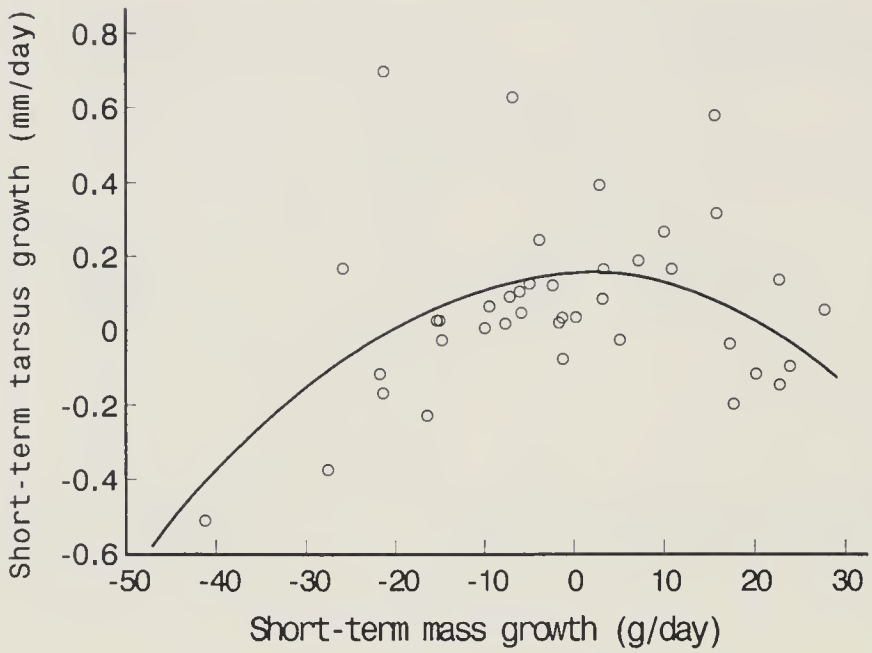

FIG. 4. Relationship between short-term tarsus growth and short-term mass growth (see Fig. 2; curve shown: $y = 0.15 - 0.0003x^2$, $F = 10.1$, $P = 0.003$).

spond to chicks recovering mass after a period of fasting, as we found a negative correlation between individual mass growth rates and short term mass growth ($r = -0.5$, $N = 30$, $P < 0.005$). Thus, the greatest mass increases were detected in chicks that suffered prolonged fasting periods. These results suggest that, after a period of fasting, there could be a delay in the recovery of normal blood levels of alkaline phosphatase, the chicks quickly recovering mass before resuming skeleton growth at the normal rate. Also, this lends support to the existence of compensatory growth after fasting periods, as has been recently demonstrated in an experiment with captive breeding American Kestrels (*Falco sparverius*; Negro et al. 1994).

The decrease in the growth rates of Red Kite chicks under conditions of food scarcity could reduce metabolic expenses and explain why we did not find any relationship between short-term growth rates and urea levels. However, urea levels were negatively correlated with long-term mass condition. Chicks with more delayed growth (lowest long-term mass condition values) are probably those suffering more protracted previous fasting periods, those in which protein catabolism had to be activated to guarantee survival during a long fasting period (high urea levels).

Variation in the duration of the nestling period mainly reflects variation in growth rates (Bortolotti 1986, Viñuela and Bustamante 1992). Growth rates of chicks of Imperial Eagles were less variable, but as indicated by urea levels, their metabolism was also more sensitive to situations of food

scarcity. These results suggest that the ability of the chicks to reduce growth rate to provide energy savings for self-maintenance is better developed in Red Kites than in Imperial Eagles. A well-developed ability to retard growth may be especially important for chicks of species with a very irregular and unpredictable food supply, such as the Red Kite (Delibes and Garcia 1984, Veiga and Hiraldo 1990). In such a situation, growth works as a 'fine-tuning' system to regulate productivity (Veiga and Hiraldo 1990). In contrast, growth delay would be unfavorable for chicks of a species that feeds on a more regular and predictable food supply but experiences strong intrabrood competition eventually leading to fratricide (Meyburg 1974, González 1989). Consequently, our results support the Growth Optimization Hypothesis and agree with the prediction by O'Connor (1978) that species feeding on more unpredictable and irregular food sources should have a more flexible growth pattern.

We do not know if the regulation of alkaline phospatase blood levels in the Red Kite is active or passive, as defined by Callow and Townsend (1981). The levels of this enzyme may be regulated by growth hormone or by other related hormones (Brown et al. 1983, Kan and Cress 1987), supporting the existence of active regulation. Alkaline phosphatase is essential to the process of skeletal growth, as opposed to mass growth, and is susceptible to hormonal control. It could be, as suggested by our results, a key physiological mechanism of growth regulation.

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NEST-SITE CHARACTERISTICS AND NESTING SUCCESS OF THE MALABAR GRAY HORNBILL IN THE SOUTHERN WESTERN GHATS, INDIA

DIVYA C. MUDAPPA[1] AND RAGUPATHY KANNAN[2]

ABSTRACT.—We quantified and characterized the nesting habitat of Malabar Gray Hornbills (*Tockus griseus*) Dec. 1993—May 1994 in the Anaimalai Hills of southern Western Ghats, India. Twenty-six nest-site variables were recorded in each of 27 nest plots to evaluate variability of nest-site selection. Malabar Gray Hornbills selected nest trees of significantly larger diameter at breast height (DBH 60–89 cm), and greater height of the lowest limb than the associated values from randomly chosen trees. The number of trees of 60–74 cm DBH class was significantly higher in the nest site plots than in the random plots. Most nests were in tall live trees and were formed primarily by heart rot where a branch had broken. Comparison of relative abundance of potential nest cavities and availability of trees in different DBH classes in belt transects indicates that more cavities were formed in trees of larger diameter. Density of potential nest cavities was 10/ha. Malabar Gray Hornbills consistently chose smaller trees than sympatric Great Hornbills (*Buceros bicornis*). This study indicates the need of mature moist forest habitat for nesting by the Malabar Gray Hornbill. *Received 13 Oct. 1995, accepted 14 Feb. 1996.*

The Malabar Gray Hornbill (*Tockus griseus* = *Ocyceros griseus*), the smallest of nine species of Indian hornbills, is endemic to the heavy rainfall tracts of the Western Ghats in southern India. It occurs commonly from Khandala in the north to the tip of the peninsula, from foothills to an altitude of about 1600 m above mean sea level (Ali and Ripley 1987). The preferred habitat of the species, moist deciduous and evergreen forest, has diminished and has become fragmented over much of the Western Ghats during the last century (Chattopadhyay 1985, Nair 1991). In the Anaimalai hill ranges of the Western Ghats, the Malabar Gray Hornbill occurs sympatrically with the largest Indian hornbill, the Great Hornbill (*Buceros bicornis*). These species are useful indicators of primary moist forest habitat.

Like other hornbills, the nesting female Malabar Gray Hornbill seals itself inside natural tree cavities until just before the fledging of the chick. Hornbills are secondary cavity nesters, i.e., they nest in large tree cavities naturally formed by decay or excavated by primary cavity nesters such as woodpeckers. They show high nest-site fidelity, returning to the same tree year after year (Kemp 1978). Many studies of Southeast Asian hornbills have stressed that they require extensive tracts of mature forest hab-

[1] Salim Ali School of Ecology, Pondy Univ., Pondicherry 605014, India. (Present address: Wildlife Institute of India, P.O. Box 18, Dehradun 248001, India.)
[2] Dept. Biological Sciences, Univ. Arkansas, Fayetteville, Arkansas 72701, U.S.A. (Present address: Dept. Biology, Westark Comm. College, Fort Smith, Arkansas 72913). Corresponding author.

itat with large, tall canopy trees for foraging and nesting (Kemp and Kemp 1975, Leighton 1982, Leighton and Leighton 1983, Johns 1987, Kannan 1994, Poonswad 1995). Cody (1985) suggested that the availability of suitable nest sites may play a major role in the population dynamics of cavity nesters. In this paper we describe the nesting habitat requirements of the Malabar Gray Hornbill by comparing nest-tree centered plots with random plots, thus identifying the factors influencing nest-site and nest-cavity selection. We also evaluate the nesting success of the species in the study area and compare nesting habitat requirements of the Malabar Gray Hornbill with that of the sympatric Great Hornbill.

STUDY AREA AND METHODS

The study was conducted in the Indira Gandhi Wildlife Sanctuary (approximately 10°25′N; 76°58′E) in Tamil Nadu state of India, which is spread over 1250 km^2 in the Anaimalai Hills of the southern Western Ghats. The altitude ranges from 315–2500 m. The Karian Shola National Park, where most of the observations were made, is a 5.1 km^2 patch of Southern Tropical Wet Evergreen Forest (Champion and Seth 1968) at an altitude of 750 m. This forest is surrounded by bamboo and open deciduous forests. The mean annual rainfall is 1400 mm, obtained from the southwest (June–Sept.) and the northeast (Oct.–Dec.) monsoons.

We made field observations from December 1993 to May 1994, during the breeding season of the Malabar Gray Hornbill (Ali and Ripley 1987). Hornbill nests were found by following parent birds and checking for piles of seeds and fecal matter (middens) at the base of nest trees. A tribal guide also showed us traditional nests. The habitat quantification methods followed James and Shugart (1970) with modifications to suit tropical forest conditions, and was similar to that of Kannan (1994) on the Great Hornbill, thus making the two data sets comparable. Ten vegetational parameters and nine nest cavity parameters were quantified in 15-m circular plots (0.07 ha) with the nest tree in the center. Vegetational parameters were also quantified in similar plots located at random 75 m from the nest tree to measure parameters in the general habitat. At the random points, the nearest tree ≥20 cm DBH was taken as center of the plot. Comparison of random plots with nest-tree plots were made to determine parameters likely to affect choice of nesting habitat by the Malabar Gray Hornbills. We used non-parametric Wilcoxon two-sample tests to determine significant differences ($P < 0.05$), using standard SPSS software (Norusis 1990, Table 1), as only three of the 10 vegetational parameters were distributed normally. Nest-cavity orientation was tested for nonrandomness using the goodness-of-fit of the Poisson distribution (Zar 1984). Twenty-seven nests were observed during this study. Each of the nests was examined at regular intervals to determine nesting status. Nesting was considered successful if at least one chick fledged or if the nest was found to be active at the termination of the study in May 1994. To determine the availability of potential nest cavities for the hornbill, five belt transects of 200 m × 100 m (i.e., total of 1 ha) were laid at random. All trees ≥30 cm DBH were carefully scanned, using 7 × 50 binoculars, for the presence of potential nest cavities (entrance diameter ≥ 6 cm). Classification of trees into DBH classes and other cavity parameters was the same as that used in the plots for nesting habitat quantification.

RESULTS

Nesting habitat characteristics.—Most of the nests were in open, tall (average height = 24 m), evergreen forest with dense undergrowth. Only

TABLE 1
MEASUREMENTS OF MALABAR GRAY HORNBILL NEST CAVITY PARAMETERS

Parameters	Mean	Standard error	N[a]
Diameter at nest height (cm)	42.4	2.1	26
Cavity width (cm)	8.3	0.3	27
Cavity length (cm)	8.4	0.3	27
Cavity height (m)	16.5	0.9	27
Distance to nearest branch (m)	1.8	0.2	27
Distance between cavity and canopy (m)	11.1	1.0	27

[a] Number of nest trees.

three parameters differed significantly between nest-site plots and random plots ($P < 0.01$; Table 2). These were DBH, the height of the lowest branch, and the number of trees of 60–74 cm DBH within the plot. The number of trees of 90–104 cm DBH also was higher in the nest plots ($P < 0.1$). Mean DBH of nest trees (75 cm) was larger than that of center trees of random plots (46 cm). The mean height of the first branch from the ground also was significantly higher in nest trees (16 m vs 11 m). Twenty-two (81%) of the 27 nests were on emergent trees, while only 13 (48%) of center trees of random plots were emergent, the mean emergence of nest plots being 4 m, 3.5 m higher than in the random plots. Similarly, while 21 of the nest trees were the tallest in the nest plots, only 6 of the center trees were the tallest in the random plots. However, the mean height of the tallest tree tended to be greater in the random plots. The DBH of the nest tree and its height were correlated ($r = 0.438$, $P = 0.02$), and the latter was in turn correlated to the height of the lowest limb ($r = 0.626$, $P < 0.001$). The foregoing variables reflect the Malabar Gray Hornbill's choice of large trees for nesting.

Since the frequency distributions of trees of various DBH classes in the nest-site plots and random plots were similar, the data were pooled for analysis. To examine whether hornbills were nesting selectively in trees of a particular DBH, the frequencies of nests in trees of predetermined DBH classes 20–39 cm, 40–59 cm, 60–79 cm, 80–99 cm, 100–119 cm, and >120 cm were compared with the pooled frequency of trees in these DBH classes. The nest tree DBH deviated significantly from random (Fig. 1, Kolmogorov-Smirnov two-sample test, $D = 16/27$, $P < 0.01$). Trees in the 60-89 cm range particularly appear to be preferred; 12 (44%) of the 27 nests were in such trees, although only 81 (19%) of the trees in the nest plots were in this range. Six (22%) of the nests were in trees of DBH >90 cm and nine (33%) in trees of the 30-59 cm range

TABLE 2

COMPARISON OF PARAMETERS IN MALABAR GRAY HORNBILL NEST-SITE PLOTS AND RANDOM PLOTS

Parameters	N	Nest plots[a]	Random plots[a]	Z	*P*
Shrub density/60 m^2	26	69.4 (5.2)	61.6 (6.0)	−1.18	0.238
Canopy cover %	26	85.2 (2.3)	83.6 (2.2)	−0.73	0.466
Ground cover %	26	28.9 (2.8)	38.3 (4.2)	−1.35	0.179
Mean canopy ht. (m)	27	23.9 (0.8)	24.7 (1.4)	−0.82	0.420
Tallest tree (m)	26	28.4 (1.4)	33.0 (1.7)	−1.71	0.087
Center tree ht. (m)	27	27.7 (1.4)	25.1 (1.4)	−1.28	0.201
Center tree DBH (cm)	27	75.3 (5.3)	45.7 (5.0)	−3.21	**0.001**
Distance to large tree (m)	26	7.1 (1.0)	8.2 (0.9)	−0.32	0.751
Lowest limb (m)	27	15.7 (0.9)	10.5 (1.1)	−3.77	**0.000**
Tree emergence (m)	27	3.8 (1.0)	0.3 (1.7)	−1.79	0.073
Number of trees					
15–29 cm DBH	27	7.5 (1.0)	9.5 (1.1)	−1.01	0.313
30–44 cm DBH	27	3.8 (0.4)	3.0 (0.4)	−1.26	0.206
45–59 cm DBH	27	1.8 (0.2)	2.3 (0.4)	−0.86	0.390
60–74 cm DBH	27	1.4 (0.2)	0.4 (0.1)	−3.11	**0.002**
75–89 cm DBH	27	0.5 (0.2)	0.3 (0.1)	−1.24	0.214
90–104 cm DBH	27	0.6 (0.1)	0.2 (0.1)	−1.73	0.083
≥105 cm DBH	27	0.5 (0.2)	0.6 (0.1)	−0.28	0.776

Differences were tested using Wilcoxon Signed 2-Sample Test for 2-tailed significance at $P < 0.1$ (Underlined) and $P < 0.01$ (Bold and underlined).

[a] Mean ± SE; N = Number of sample plots.

(Fig. 1). A comparison of the relative abundance of potential nest cavities and the availability of trees in different DBH classes in the belt transects indicates that more cavities are formed in trees of larger diameter (>60 cm).

Nest cavity characteristics.—Nest cavities were located at an average height of 16.5 m, and the average diameter of the nest entrance was about 8 cm. Mean diameter at nest height (DNH) was estimated to be 42 cm (N = 27). The cavity entrance was circular in 25 of 27 nests and oval in the other two. The mean width and length of the cavity entrance, distance of the cavity to the nearest branch, and distance between the cavity and canopy were also calculated (Table 1). All cavities except one were in live trees. Twenty-one (78%) of the nests were apparently formed as a result of heart rot where branches had broken off, while others were excavated by primary hole nesters. Sixteen (59%) of the nests were on the main trunk and the rest on branches. A majority (59%) of the nest cavities were located on the middle third of the tree, i.e., 9–18 m high,

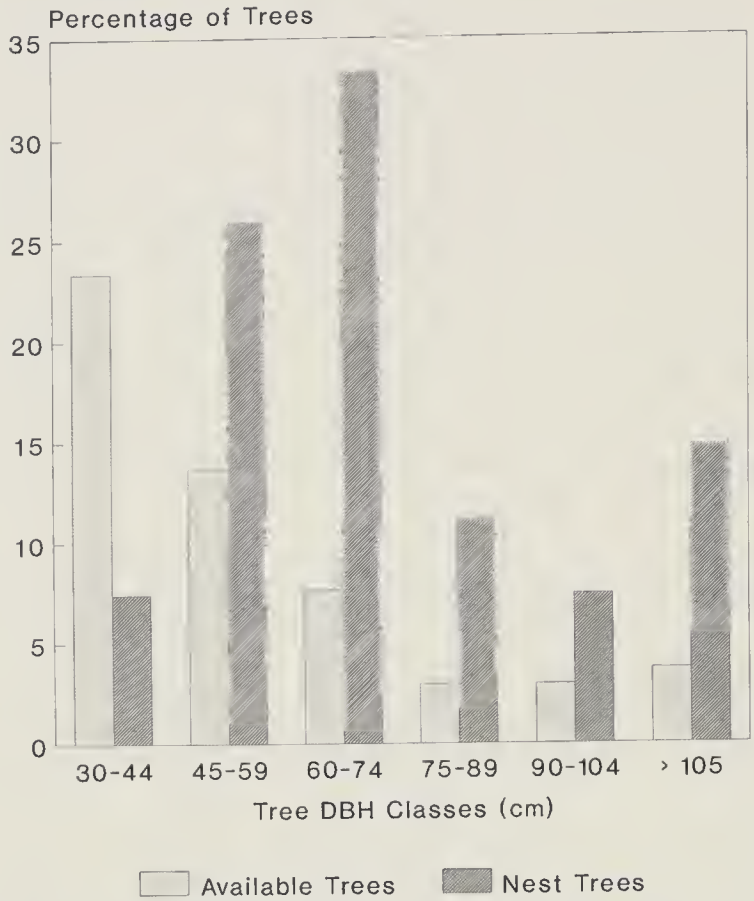

FIG. 1. Frequeney distribution of DBH values of available trees and nest trees.

followed by 33% in the upper third (>18 m) and only 7% in the lower third (<9 m). There was a significant difference in the degree of orientation of the nest cavities (χ^2 = 12.14, df = 3, P = 0.01). A higher proportion of both the active and potential nest cavities in the limited sample available in the 1 ha area were oriented in the northeast direction (Figs. 2A and 2B).

Of 157 trees above 30 cm DBH in the 1-ha area sampled, only 10 had cavities potentially suitable for the Malabar Gray Hornbill. A comparison of the presence of nests and availability of nest cavities in trees of three different DBH classes (30–59 cm, 60–89 cm, and >90 cm) showed that hornbills were using trees of these DBH classes more or less according to their availability (χ^2 = 3.45, df = 2, P > 0.1). Three of the four tree species used most frequently for nesting occurred in the 1-ha plot that

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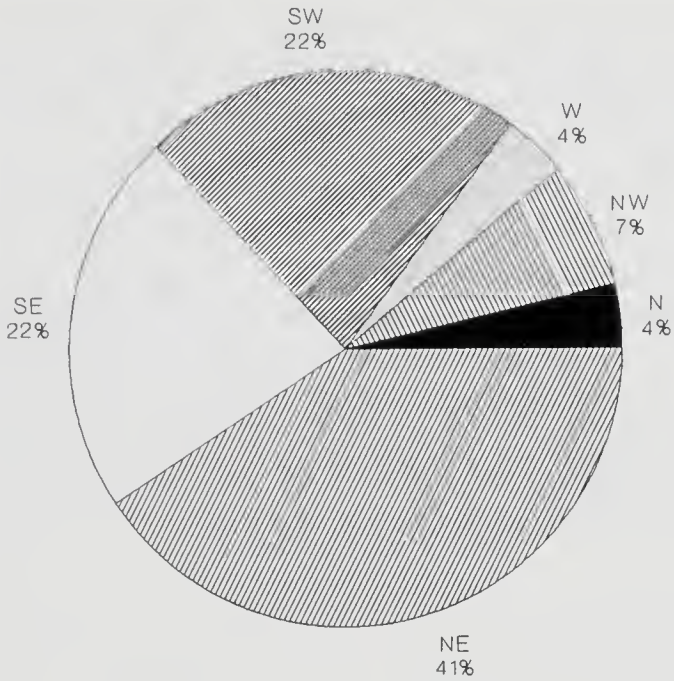
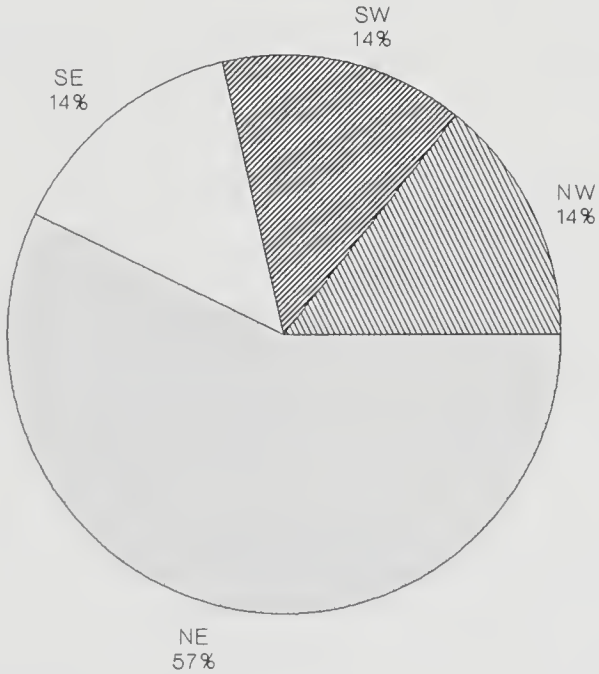
FIG. 2. (A) Orientation of nest eavities of Malabar Gray Hornbill nests (N = 27). (B) Orientation of potential nest eavities of the Malabar Gray Hornbill in one ha (N = 7).



A



B

was sampled (*Alseodaphne semecarpifolia, Hopea parviflora, Aglaia roxbhurghiana*). Seven of the 27 nests were in *A. semecarpifolia* trees.

Nest-cavity dimensions.—One nest of the Malabar Gray Hornbill which was at a height of 22.2 m was examined on 1 March 1994. The interior dimensions were 25 cm (width) × 36 cm (depth). The DNH of the tree was estimated to be 65 cm. The cavity extended into the interior of an adjoining branch forming a "funk hole" (i.e., an extension of the cavity into another branch or higher up into the bole) into which the incubating female withdrew. The measurement along this axis was 63 cm. The cavity had no particular inner lining although wood dust with some seeds were obtained. A single egg was present. The off-white, smooth, and slightly dirty egg measured 4.5 × 3.5 cm. On 5 March, the female resealed the cavity. By 22 March, the chick had hatched and egg shells were found in the midden.

Nesting success.—Of the 27 nests monitored, 14 successfully fledged young and 10 were active at the end of the study period. Of the remaining three nests, one was abandoned in mid April 1994, one could not be observed due to poor visibility, and the other was not used in 1994 for nesting (this nest was active during the preliminary survey in May 1993). Overall, 24 (88.9%) of the 27 nests were considered successful.

DISCUSSION

Cavities are an important resource in forests for many birds and mammals which use them for nesting, roosting, and escaping from predators. To a certain extent, the choice of cavities may also depend on the faunal community, especially in terms of avoiding interspecific competition for nest sites and food (Kalina 1988, Li and Martin 1991, Conway and Martin 1993), predation (Kemp 1976, Cody 1985, Martin 1988), and presence of adequate foraging habitat (Conner 1976). However, nest-tree and nest-cavity factors may be the most important primary factors influencing nest habitat choice in hornbills (Kannan 1994).

Nest-site selection.—Nests of the Malabar Gray Hornbill were found in open, tall evergreen forest along forest trails, edges and interior areas. The data obtained reflect size and age of nest trees and indicate that hornbills prefer mature forest stands. Although most of the nest cavities were in emergent trees, they were not necessarily the tallest trees in the habitat. The Malabar Gray Hornbill uses relatively smaller trees than the sympatric and much larger Great Hornbill which was found to prefer nests in trees that were larger in terms of mean height (43.8 m), emergence (12.8 m), DBH (133 cm), and DNH (79 cm) (Kannan 1994). It is, therefore, evident that there is little overlap in nesting habitat choice between the two sympatric hornbills in the study area.

Relatively more nests were found in trees of larger DBH classes, particularly in the 60-89 cm range. This cannot be taken to indicate the preference of the hornbills, as it may simply reflect the greater availability of suitable cavities in larger trees. A large number of nests (26) were in live trees. The potential nest cavities located in the 1-ha plot were also in live trees. Selective logging of trees is usually directed towards the extraction of large rain forest species for timber and prioritizes removal of trees with cavities, heart rot, and strangler species (*Ficus*) as unwanted during silvicultural operations. Such activities continue in many areas in the Western Ghats, even within protected areas. These trees are essential for the Malabar Gray Hornbill as potential nesting sites. Large fruiting trees were also shown to be an important component of hornbill habitat (Kannan 1994). Therefore, this is a consideration that should be incorporated in traditional forestry practices.

Nest-cavity characteristics.—The nests of the Malabar Gray Hornbill were located at substantial heights in evergreen forest trees. Height at which the nest is located may simply reflect the fact that nest cavities are formed more frequently in the higher reaches of the tree. The propensity of the hornbill to choose cavities with small entrances is supported by observations on conspecifics in Africa (Kemp 1976, 1978). One nest, active in 1993 but abandoned the following year, had a cavity entrance diameter of 15 cm, suggesting that tree growth could have enlarged the cavity, thereby rendering it unsuitable for nesting. Many hornbills were seen assiduously enlarging the nest cavity entrance by removing overgrown wood tissue and debris. "Funk-holes" of the type discovered in this study have been reported by Kemp (1978) for most hornbills in the African and Oriental regions.

Nesting success.—Higher nests suffer lower amounts of predation in both primary and secondary cavity nesters (Li and Martin 1991). In hornbills, further protection is afforded by the sealed nest cavity entrance and the presence of the confined female. The low incidence of predation and the presence of suitable nesting habitat probably accounted for the high nesting success noted in this study. In general, nesting success in hornbills is probably one of the highest among hole nesters, by virtue of their unique nesting behavior. The importance of preserving cavities in large trees for hornbills is evident from this as well as several other studies (Leighton 1982, Ali and Ripley 1987, Kannan 1994).

Hornbills play an important role in forest dynamics because they disperse seeds of many forest trees, especially the large seeded ones (McKey 1975, Leighton and Leighton 1983), and may serve as "mobile links" (Gilbert 1980) in the food-web organization of rainforests (Kannan 1994). Loss of habitat due to conversion of primary forests into plantations and

monocultures, especially of exotics such as *Tectona grandis*, *Eucalyptus*, and *Acacia* may adversely affect survival of these large forest birds. Thus, the conservation of hornbills assumes greater importance in preserving the entire threatened ecosystem of the Western Ghats.

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SIBLICIDE IN SWALLOW-TAILED KITES

RICHARD P. GERHARDT[1], DAWN M. GERHARDT[1], AND
MIGUEL ANGEL VASQUEZ[2]

ABSTRACT.—We studied the reproductive behavior of Swallow-tailed Kites (*Elanoides forficatus*) in northern Guatemala. Modal clutch size was two (range 1–2), but no nests succeeded in fledging more than one young. Eggs were laid at intervals of three to four days and hatched at intervals of three to five days. Second eggs weighed significantly less than first eggs. Second chicks either received no food or obtained so little that they did not grow. First chicks vigorously attacked their nestmates, and all second chicks died within five days of hatching. Food stress was not found to be a proximate cause of this behavior. Siblicide appears to be innate in this population of Swallow-tailed Kites, even though the northern subspecies does not exhibit this behavior. Swallow-tailed Kites are, in certain aspects, an anomaly among species within the order Falconiformes that exhibit obligate siblicide. *Received 26 March 1996, accepted 29 Sept. 1996.*

Siblicide is known to occur in numerous raptor species as well as in egrets (Mock 1985), gannets (Jarvis 1974), boobies (Drummond 1986, Anderson 1990), skuas (Procter 1975), pelicans (Cash and Evans 1986), kittiwakes (Braun and Hunt 1983), and other birds. Among raptors, this phenomenon is most common in eagles (Brown 1966, Edwards and Collopy 1983, Gargett 1993).

There are two subspecies of Swallow-tailed Kites, (*Elanoides forficatus*). *E. f. forficatus* migrates from South America to breed in the southeastern United States. Numerous breeding studies have been conducted on this northern subspecies (Snyder 1974, Meyer and Collopy 1990, Cely and Sorrow 1990). Modal clutch size is two, and as many as three young have been reared successfully; two young fledge frequently. A single case of apparent siblicide has been documented for this subspecies (Sutton 1955); the smaller of two young died in week four after being injured and kept from food by its larger nestmate. *E. f. yetapi* occurs in Middle and South America with northern populations being migratory. In Tikal National Park, Guatemala, near the northern edge of the range of this subspecies, Swallow-tailed Kites have never been known to raise more than one young, and two-egg clutches have not been reported previously. In 1990 and 1991, we undertook a study in Tikal in which we regularly climbed to nests to determine the number of eggs and young, and conducted all-day observations at several nests. The results of that study are presented here with particular reference to siblicide.

[1] The Peregrine Fund, Inc., 5666 West Flying Hawk Lane, Boise, Idaho (Present address: 341 NE Chestnut St., Madras, Oregon 97741).
[2] El Parque Nacional Tikal, El Petén, Guatemala.

STUDY AREA AND METHODS

Tikal National Park is in the Department of El Petén, in northern Guatemala (17° 13′N, 89°38′W), where the semi-deciduous, lowland forest is classified as part of the Tropical Dry Life Zone (Holdridge 1957). Average annual rainfall is approximately 1.4 m (Smithe 1966); the area experiences distinct wet and dry seasons, the latter being from January to June. The main Maya ruins around which the park was established are on a limestone hill that is the highest point (250 m) for a considerable distance. This hill supports a dense concentration of nest sites of this loosely colonial species, and the ruins provided vantage points from which we found and observed the kites' treetop nests. We observed nest-building and courtship activities and, once a female began to spend more than an hour in an incubating posture, we climbed to the nest to verify the clutch.

We visited each nest every second or third day until the clutch was completed and then again when we expected hatching to occur. In some cases we were able to climb all the way to the nest; otherwise, we used a small mirror fixed to a pole to examine nest contents. Where possible, we measured and weighed eggs (within two days of laying) and young (periodically after hatching). We compared the mass of first eggs and second eggs using the Mann-Whitney *U* test (Zar 1984). Values throughout are means ± standard deviations.

We observed certain nests, selected for visibility, every third day throughout the incubation and nestling periods. Observations began 30 min before sunrise and ended 30 min after sunset. We recorded behavior of adults and young and the number and type of prey delivered to nests.

RESULTS

Swallow-tailed Kites placed their nests in the tops of the tallest emergent or lone trees. Mean tree height was 32.6 ± 4.8 m and mean nest height was 30.3 ± 4.8 m (N = 22). Nests were made of dead branches and vines; the nest cup was formed using *Usnea* lichens and Spanish moss (*Tillandsia usneoides*). Eighteen nests were found prior to or during incubation (nine each year). Fifteen eventually contained two eggs each; three held one egg each, giving a mean clutch size of 1.83 eggs.

Eggs within a clutch were laid three to four days apart and incubation began after the first egg was laid. Mean incubation period was 31.5 ± 0.9 days (N = 6 eggs for which laying and hatching dates were verified by climbing). At nine nests (five in 1990, four in 1991), both eggs hatched, with hatching intervals of three to five days. At eight of these nine nests, the second chick died when between three and five days old. In the ninth nest, both chicks were taken by predators on day four of the second chick's life; this chick was clearly dying when the breeding attempt failed.

One nestling fledged successfully from six of the 18 nests, four in 1990 and two in 1991. Thus, 33% of nesting attempts were successful, and 0.33 young fledged per nesting attempt (i.e., nests with eggs laid; N = 18). During this study, 1.00 young fledged per successful nest (N = 10, including four additional 1991 nests found during the nestling period); numerous anecdotal observations in years prior to and after the study

agree with this figure. In all six of the successful nests we observed, it was the first egg that produced the successful fledgling. In one of the 18 nests found during incubation, the second egg survived after the first fell out of the nest. Until the eventual failure of this breeding attempt, the second egg represented the only chance for success at this nest.

Second eggs ($\bar{x}$ = 33.6 ± 3.4 g, N = 5) were significantly smaller than first eggs ($\bar{x}$ = 40.7 ± 2.1 g, N = 4; U = 20, P = 0.02). Two first chicks weighed on day two had body masses of 41 and 37 g. Two second chicks had day-two body masses of 22 and 25 g, when their respective nestmates had body masses of 68 g (day five) and 93 g (day six).

We were able to observe siblicidal behavior at eight of the nine nests in which two eggs hatched. We conducted all-day observations at seven of these nests. In all cases, the first-hatched chick (A-chick) was seen attacking its younger nestmate (B-chick). This began shortly after B-chicks hatched and continued intermittently until their death. Most frequently, A-chicks pummeled B-chicks with their bills, with blows directed toward the head and neck. In addition, A-chicks grabbed B-chicks with their bills, pulling with an up-and-sideways wrenching motion. This latter maneuver was often directed at the head and neck, but occasionally a wing or back was treated in this manner. There was no battle; the undersized second nestlings never fought back or displayed any effective defence.

Aggressive attacks came in bouts lasting from a few blows to approximately 30 minutes. This behavior occurred both when the chicks were alone and when one of the adults was present. Although it was difficult to observe, we believe that brooding by a parent prevented the continuance of these attacks. Adults did not, however, intervene to stop attacks. A-chicks attacked B-chicks both when food was present and when food was absent. In some cases, attacks continued in spite of prey deliveries. Thus, the presence of food did not seem to stimulate aggressive behavior in A-chicks. Begging by B-chicks appeared to stimulate aggression from their nestmates. A prone and silent B-chick was much less likely to be attacked than one that was upright and calling. Nonetheless, B-chicks continued raising themselves and vocalizing as long as strength permitted.

It is difficult to identify with certainty the cause of death of the younger nestlings. The blows inflicted by their siblings did not lacerate the skin but may have caused some internal bleeding. The continued attacks weakened B-chicks to the point where they could no longer raise themselves to receive food. Moreover, they received little or no food to begin with; since the aggression of their older nestmates often placed them in a subordinate position when a parent arrived with prey. If individual B-chicks managed to receive food, it did not result in weight gain. Death always

occurred while they were not yet mobile enough to move to the edge of the nest and while A-chicks were not yet strong enough to push or pull them to the edge. We do not believe any B-chicks died as a result of falling from the nest. We suspect that starvation, possibly combined with internal injuries, caused the death of younger chicks.

We watched the death of the B-chick at one nest, where the young hatched three days apart. Four days after the second chick hatched, its older sibling attacked it throughout the morning and early afternoon. At first, the B-chick continued to raise itself, and its peeping seemed to provoke further attacks. It received no food during the entire day and grew weaker as the day progressed. By nightfall, it had been some time since it had raised his head; we believed it to be dead. We arrived at the observation point early the next day. As soon as the female, who had spent the night on the nest, awoke, she began picking at and eating the dead young. After taking several bites, however, she flew from the nest with the carcass and let it fall through the canopy.

Our observations did not indicate that food shortage (or competition) is a proximate cause of siblicide in this population of kites. Sibling aggression was not triggered by prey deliveries, and siblicide occurred at an age at which the food required by the brood of two was a small fraction of the food requirements later in the nestling period (Gerhardt et al., unpubl. data). Aggression continued unabated even when the A-chick was apparently satiated and refused further food. Siblicide and the associated aggression occurred predictably and regularly in both nesting seasons in which we conducted this study, and no nests of this population have been known to fledge two young in many years of casual observations prior to and following our study.

Two other isolated observations bear recounting here. At one nest at which we conducted focal observations, the second egg failed to hatch. The single young at this nest was observed pummeling this egg just as other A-chicks pummelled their siblings. We do not suggest that this behavior caused the egg to fail. Rather, we feel that this observation illustrates the degree to which aggressive behavior toward a nestmate is innate in these birds. Another nest that we observed closely was much delayed relative to other nests (and, we believe, represented a renesting attempt). At this nest, siblicide took place (a seven-day-old nestling killed its four-day-old sibling) at a time when other pairs of kites were delivering prey to single chicks nearly ready to fledge (40+ days after hatching). That is, single young were receiving ten or more prey items (invertebrates and vertebrates) with a total biomass in excess of 70 grams (Gerhardt et al. unpubl. data). Thus, prey availability at the time of this siblicide was much more than sufficient to provision the two young at this late nest.

DISCUSSION

Detailed descriptions of the behavior of young have been published for only four species of siblicidal falconiforms. Swallow-tailed Kites in Tikal are similar to Black Eagles (*Aquila verreauxii*; Gargett 1993) and unlike Lesser Spotted Eagles (*A. pomarina*; Meyburg 1970) in that B-chicks apparently do not alter their behavior in response to aggression from their nestmates. As in the kites we observed, neither Black Eagle nor African Hawk Eagle (*Hieraaetus fasciatus*; Meyburg 1974) B-chicks flee from this persecution; Lesser Spotted Eagle chicks do. At no time in their short lives did second Swallow-tailed Kite chicks exhibit normal growth.

Edwards and Collopy (1983) defined siblicidal species as "obligate" when the phenomenon occurs invariably and as "facultative" when it occurs occasionally. Simmons (1988) defined "cainism" as siblicide in the absence of food shortage and considered it obligate if occurring in more than 90% of cases. In accordance with these definitions, the Tikal population of Swallow-tailed Kites exhibits obligate cainism. Moreover, the siblicide we witnessed is also obligate when considering Gargett's (1993) argument that the distinction is absolute rather than relative. She stated that in facultatively siblicidal species the competition is for food, and death of the second chick is incidental to the struggle. For the kites we studied, as in the Black Eagles she studied, the immediate objective of the A-chick appears to be the death of its nestmate.

Our research allows us to add Swallow-tailed Kites to the ranks of known siblicidal birds. This finding is of particular interest both because Swallow-tailed Kites are an anomaly among obligately siblicidal falconiforms and because they exhibit intraspecific variation in the nature of this life-history strategy.

Traits that this population of Swallow-tailed Kites shares with other siblicidal falconiform species include a tropical distribution, a maximum clutch size of two (Simmons 1988), a longer hatching interval, and a greater difference in egg and hatching mass (Edwards and Collopy 1983) than species that are facultatively siblicidal.

Swallow-tailed Kites differ in many respects, however, from other obligately siblicidal species within this order. Most are large; the next smallest obligately siblicidal falconiform is the Augur Buzzard (*Buteo augur*; Gargett 1970a), which at 1100 g (female mass) is more than twice as heavy as a Swallow-tailed Kite. Other species that exhibit obligate siblicide have a delayed acquisition of adult plumage (Simmons 1988). Swallow-tailed Kites apparently acquire Definitive Basic plumage at 14–16 months (Meyer 1995), but plumage acquisition of the race *yetapi* remains poorly studied.

Such size and plumage traits are associated with longevity. This fact is an important assumption of Simmon's (1988) theory that cainism results in selection for quality and competitive ability. That is, obligately siblicidal falconiform species tend to experience extremely high subadult mortality and intense competition for breeding sites. Another concept advanced is that such species tend to be the most solitary species (Gargett 1970b, 1993). Again, Swallow-tailed Kites do not fit these trends. Little is known of the subadult mortality of this species. They do not experience intense competition for breeding sites, however, since these birds are loosely colonial, excluding other conspecifics only from the immediate nest area. Far from being solitary, Swallow-tailed Kites forage, roost, and migrate in large groups, and assist one another in nest defense (Meyer 1995, pers. obs.). Other siblicidal bird species besides falconiforms are colonial to varying degrees (Mock 1985, Cash and Evans 1986, Anderson 1990).

Whereas the population we studied exhibits obligate siblicide, no similar siblicidal episodes have been reported for the northern subspecies. The single documented case of siblicide in Florida (Sutton 1955) was probably a food-related brood reduction that occurred within the fourth week after the victim hatched. Two and sometimes three young regularly fledge from nests of this subspecies. The intraspecific variation documented here may provide a fertile area for research of the evolution of this phenomenon. To date, however, there are insufficient data from either subspecies to compare hatching success or to apply the insurance-egg hypothesis (Dorward 1962) to this species. Nonetheless, our findings prove that this reproductive strategy is not confined (within falconiforms) to the large eagles and suggest that the evolution of this phenomenon can occur at the subspecific level.

Two lines of inquiry can be pursued regarding siblicide such as this. The first suite of questions concerns the inability of such birds to raise a second young. Setting aside, for the moment, the mechanisms by which this strategy evolved, the basic answer is that the optimal brood size is (or was in the evolutionary past) one. A number of hypotheses regarding resource limitations have been put forth to explain not only siblicide but also the general trend in the tropics toward lower clutch and brood sizes than in more temperate zones (Lack 1966). Our research does little to advance such hypotheses; that brood sizes are smaller in this population of kites than in the northern subspecies is in keeping with this trend. The reproductive strategy of the sympatric Plumbeous Kite (*Ictinia plumbea*) supports the notion that some resource limits optimal brood size to one. Among raptors breeding in our study area, Plumbeous Kites are most similar to Swallow-tailed Kites in size, migratory strategy, nest placement,

feeding behavior and prey (Vásquez et al. 1992, Gerhardt, unpubl. data). This species not only fledges a single young, but lays only one egg (Vásquez et al. 1992, Gerhardt, unpubl. data).

The prey-size hypothesis (Mock 1985) proposes that small prey delivered directly to young (and thus monopolizable) can serve as a proximate trigger for sibling aggression. Young Swallow-tailed Kites are fed such prey, but it is not clear that there is any difference in this regard between the siblicidal population in Tikal and the northern subspecies, which does not exhibit siblicide (Meyer 1995). Moreover, sibling aggression in this study appeared to be independent of prey deliveries. These facts do not weaken the prey-size hypothesis but rather relegate its applicability, for this species, to the evolutionary past.

For species such as Black Eagles (Gargett 1993) and these Swallow-tailed Kites, innate aggression toward nestmates appears to be at least part of the mechanism for the continuance of siblicide. If this is the case, then a B-chick should exhibit aggressive behavior in cases where its disadvantages have been reduced or negated, either naturally or through brood manipulation experiments. We neither conducted any such experiments nor had any natural nests in which this could be tested—all B-chicks in this study were at too great a disadvantage to display such behaviors.

The second basic question concerns why, if optimal brood size is one, parents bother to lay a second egg. We can only speculate that, as in several other obligately siblicidal species (e.g., eagles, boobies, pelicans, and penguins, Dorward 1962, Warham 1975, Mock 1985, Cash and Evans 1986, Anderson 1990), a small percentage of successful fledgings in this population of kites will come from second-laid eggs, and that those eggs act as "insurance" (Dorward 1962) against loss of an entire nesting attempt should the first egg fail to hatch or result in a weak or deformed young. The "cost" to Swallow-tailed Kites of laying a second egg is clearly small, since mass of the second egg is less than 8% of female body mass and since little or no time is spent feeding second young. A much larger sample size is necessary before we can even begin to assess the "benefit" by learning how frequently second eggs result in successful fledgings.

Our results suggest that siblicide is genetically fixed to a considerable extent in this population of Swallow-tailed Kites. Behavioral observations indicate that sibling aggression occurs independent of prey deliveries and apparent hunger levels. Moreover, we have documented that this population of kites shares numerous traits (long hatching interval, difference in egg and hatching mass, regular and predictable nestling behaviors and siblicide) with other obligately siblicidal species for which food shortage has not been shown to be a proximate trigger (O'Connor 1978, Stinson

1979, Mock 1985, Gargett 1993). These findings do little to advance our understanding of the exact mechanisms responsible for the evolution of this reproductive strategy. Nonetheless, the knowledge that this strategy is employed by a small, gregarious species that differs in many respects from other obligately siblicidal raptors may slightly redirect efforts to explain the evolution of this phenomenon within the falconiforms.

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HABITAT SELECTION OF LEWIS' WOODPECKERS IN SOUTHEASTERN COLORADO

KERRI T. VIERLING[1]

ABSTRACT.—Lewis' Woodpeckers (*Melanerpes lewis*) on the plains in the Arkansas River valley and in the foothills of the Wet Mountains in southeastern Colorado used large, dead or decaying broadleaf cottonwoods (*Populus deltoides*) for breeding and for winter mast storage. On the plains, they nested near fallow and mowed fields, but avoided anthropogenic structures and grazed fields. During the 1992–1993 winter, woodpeckers occupied sites near corn fields, and stayed on these sites into the 1993 breeding season. In the foothills, they avoided dense stands of trees at all times of year, nested near grazed fields, and wintered near oaks. Riparian habitats were particularly important to Lewis' Woodpeckers in southeastern Colorado, especially those with large mature cottonwoods. *Received October 26, 1995, accepted 1 Sept. 1996.*

Lewis' Woodpeckers (*Melanerpes lewis*) were placed on the Audubon Society's Blue List for 1975 (Arbib 1974), and local population declines have been recorded in Utah and in British Columbia (Behle et al. 1985, Sorenson 1986, C. Siddle, pers. comm.). Atypical of most picids, these birds flycatch during the breeding season and store mast in the winter (Bock 1970). Although others have described their breeding and winter habitats (Bent 1939, Bock 1970, Hadow 1973, Sousa 1982), no studies have quantified specific attributes of occupied versus random sites for this bird during either the breeding or winter season. The objective of the present study was to determine the habitat requirements for this species during the breeding and winter seasons in southeastern Colorado by comparing occupied site characteristics with random site characteristics. The specific aims of the project were (1) to quantify nest tree, nest cavity, and storage tree characteristics and compare these to random tree characteristics, (2) to characterize the breeding season habitats surrounding nest trees and random trees, and (3) to characterize the winter habitat surrounding storage trees and random sites, with an examination on the effect of mast on the winter site selection.

METHODS

I studied woodpeckers in 1992–1993 at two riparian woodland sites in southeastern Colorado. One site was on the plains of the Arkansas River Valley (38°05′N, 103°45′W, 15 km from Rocky Ford, elev. 1285m) and was intensively farmed and/or grazed. The second was in the foothills of the Wet Mountains (38°05′N, 104°58′W, 15 km from Beulah, elev. 1939 m) and supported moderate livestock grazing. During the breeding seasons, I measured 30

[1] Univ. of Colorado, Environmental, Population, and Organismic Biology, Campus Box 334, Boulder, CO 80309-0334.

nest trees on the plains and 17 in the foothills. During the winter, I measured 21 storage trees on the plains and 13 storage trees in the foothills.

I compared attributes of occupied sites with characteristics of random sites to determine whether habitat selection occurred. Occupied trees during the breeding season contained at least one nesting Lewis' Woodpecker pair, while occupied trees during the winter contained mast stores from at least one bird. Multiple Lewis' Woodpecker pairs occasionally nested in the same tree, and in these instances, the tree was used as the sample unit. Although some nest trees in 1992 were also used by the birds in 1993, these trees were excluded from the analysis. Random sites were selected by placing a pencil at spots on a 1:24000 United States Geological Survey topographic map, and by choosing the tree closest to the marked spot on the map. If a grove of trees was on the spot on the map, a tree was selected within the grove.

Tree characteristics such as the diameter at breast height (dbh), height, species, and health (live vs dead or decaying) were noted for nest trees and storage trees. Measurements for dbh were taken with a measuring tape and nest cavity orientation was measured with a compass. Nest tree, storage tree, and nest cavity heights were determined using a Suunto clinometer. Several factors were used to determine the health of occupied trees. Broken limbs are probable entry sites for heartwood decay (Conner et al. 1976, Conner and Locke 1982, Daily 1993), and these were used as an indicator of decayed trees. Additional features used to identify decaying trees included the lack of bark and leaf growth on branches, as well as visual observations of decayed wood in exposed branches. By these criteria, dead and decaying trees were distinguished readily from healthy trees that lacked all signs of decay as noted above. Similar measurements were made at randomly selected trees and comparisons made to determine if tree selection was occurring.

I quantified habitats surrounding nest trees, storage trees, and random trees by bird-centered habitat analysis (hereafter BCA; Larson and Bock 1986). Each occupied tree/random tree served as the center of a circular plot; since birds almost always foraged within 100m of the nest/storage tree (pers. obs.), I chose this as the radius of the BCA plots. I divided each BCA plot into 16 sections and assigned a single habitat type to each section: fields (fallow, grazed, or mowed), trees, anthropogenic structures, and bare ground. Corn fields and cultivated fields were additional habitat variables recorded only at the plains sites. Since cultivated fields were plowed under in the fall on plains sites, plowed fields were substituted for cultivated fields in the winter analysis. Oaks were present only in the foothills and were assigned separately from the general tree category because of their importance as a mast source.

The habitat type assigned to each plot section represented its major land cover. Typically, a plot section consisted of only a single habitat type (e.g., grazed field). However, if mixed habitat types occurred in a plot section, I assigned the habitat type which represented >50% of the land cover in that section. The frequencies of habitat types were totaled for each BCA plot; graphically, these frequencies were used to generate the average percent habitat type per BCA plot.

The effects of mast on nonbreeding habitat selection were determined by examining the presence of mast sources in relation to occupied storage trees. Since corn was the only mast available to birds wintering on the plains, I compared the frequency of corn fields in occupied BCA plots with those in random plots. Winter food estimates in the foothills were based both on the presence of oaks within BCA plots and their corresponding acorn crops. I estimated acorn crops by placing a 0.5 m^2 hoop randomly on the ground beneath a randomly chosen oak and counting the number of acorns inside the hoop. Partially buried acorns and acorn caps were not counted in the analyses, as they may have been part of the previous year's crop. Three replicates were performed per quadrant in the four BCA quad-

rants surrounding both storage trees and randomly selected oak trees (N = 12 hoops per plot).

Because the data deviated from normality, I used the Mann-Whitney *U* test (Zar 1984) to compare dbh and tree height data. I used a chi-square contingency table to compare the species and health of nest trees versus random trees. I tested the null hypothesis that there was no significant difference in the nest cavity orientation among breeding pairs with the expectation of an equal number of nest holes in the north, south, east, and west quadrants. To determine if the surrounding habitats affected habitat selection, I compared the frequency of occurrence of different habitat types between occupied and random sites using a chi-square contingency statistic (Zar 1984). I used the method of Neu et al. (1974) to determine the habitat characteristics contributing significantly to the chi-square scores. Since foothills breeding data did not differ significantly between years, these data were pooled. Plains nest season data differed between 1992 and 1993 and are presented separately. In order to examine the effects of mast on habitat selection, I compared the frequency of corn fields between occupied and random sites using Neu et al. (1974). I used the Mann-Whitney *U* test to compare average number of acorns between occupied and random sites. All data are presented as averages and standard deviations unless otherwise indicated.

RESULTS AND DISCUSSION

Nest tree and storage tree characteristics.—Forty-seven nest trees were measured over the two breeding seasons. Nest trees at both sites were taller than random trees (20.4 m ± 5.2 vs 12.5 m ± 6.4) (U = 373.0, df = 1,46, $P < .0001$) and of larger diameter than random trees (112.6 cm ± 38.8 vs 63.6 cm ± 54.9) (U = 444.0, df = 1,46, $P < .0001$). All nest trees (N = 47) were dead or decaying broadleaf cottonwoods (*Populus deltoides*) (Table 1). Nest holes (N = 59) averaged 11.1 m ± 3.4 in height (range = 5.3 m to 20.7 m), and hole orientation (N = 59) did not differ from random (χ^2 = 1.6, df = 3, $P > .50$).

Dead or decaying nest trees are important habitat components for many breeding North American woodpeckers. For instance, most nests of the Pileated Woodpecker (*Dryocopus pileatus*) (Bull 1987) and Red-headed Woodpecker (*Melanerpes erythrocephalus*) (Reller 1972) were in dead trees, while Red-cockaded Woodpeckers (*Picoides borealis*) nested only in live pine trees which possessed decaying heartwood (Ligon 1986). The soft wood of dead/decayed trees is critical for Lewis' Woodpecker breeding activities because their skulls are not adapted to drilling into hard wood (Spring 1965).

I measured 34 storage trees during the 1992–1993 winter. Trees used for mast storage differed significantly from random trees at both sites. Storage trees were taller (17.5 m ± 6.7 vs 10.9 m ± 6.0) (U = 240.5, df = 1,33, $P < .0002$) and of greater diameter than random trees (104.8 cm ± 34.8 vs 61.7 cm ± 89.2) (U = 197.0, df = 1,33, $P < .0001$). Lewis' Woodpeckers also stored mast significantly more in dead/decaying broadleaf cottonwoods (Table 1).

Among those woodpeckers which store mast, many utilize storage trees

TABLE 1
HEALTH AND SPECIES OF OCCUPIED TREES AND RANDOM TREES DURING 1992–1993 IN SOUTHEASTERN COLORADO

Season	Tree characteristics	Occupied trees	Random trees
Breeding	Health[a]		
	Dead/decaying	46	19
	Alive	1	28
	Species[a]		
	Populus sp.	46	19
	Other spp.	1	28
Winter	Health[a]		
	Dead/decaying	28	12
	Alive	6	22
	Species[b]		
	Populus sp.	27	14
	Other spp.	7	20

[a] Characteristics differed significantly ($P < 0.001$) between occupied and random trees.
[b] Characteristics differed significantly ($P < 0.005$) between occupied and random trees.

with similar characteristics. Acorn Woodpeckers (*Melanerpes formicivorus*) constructed huge granaries in dead trees with deep bark (MacRoberts and MacRoberts 1976). Similar types of trees were used by Red-bellied Woodpeckers (*Melanerpes carolinus*) (Kilham 1963) and Red-headed Woodpeckers (Kilham 1958a, b, Moskovits 1978). While Acorn Woodpeckers drilled individual holes for the storage of each acorn, Red-headed Woodpeckers, Red-bellied Woodpeckers, and Lewis' Woodpeckers all tended to use natural cavities and crevices. For Lewis' Woodpeckers in Colorado, the deep furrowed bark of cottonwoods and the presence of crevices in decaying trees may have facilitated storage of acorns.

Breeding habitat characteristics.—Habitat characteristics surrounding nest trees in the foothills differed from habitat characteristics surrounding random trees ($\chi^2 = 38.4$, df = 6, $P < .001$) (Fig. 1). Lewis' Woodpeckers nested near grazed and mowed fields, and near oaks. Light or moderate grazing occurred at this site, and lightly grazed areas contain higher densities of grasshoppers (Capinera and Sechrist 1982, Jepson-Innes and Bock 1989, Welch et al. 1991) and other insects (Lavigne and Kumar 1972) than heavily grazed areas.

Bare ground, ungrazed grasslands, and structures were all habitat types that did not occur near occupied sites in the foothills. Presumably, few insects would be present on bare ground due to the lack of vegetation.

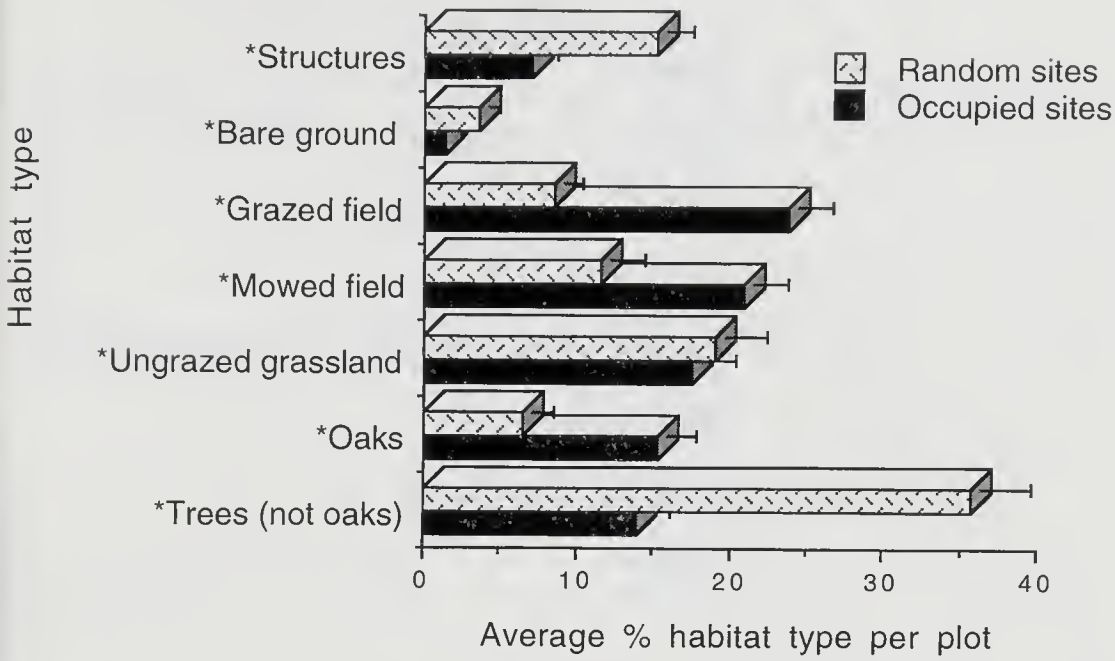

FIG. 1. Characteristics (mean percent habitat type per plot ± SD) of 100-m diameter plots surrounding 17 Lewis' Woodpecker nest trees vs 17 random trees during the 1992 and 1993 breeding seasons in the foothills of the Wet Mountains. Asterisks represent those habitat variables which differ significantly between occupied and random sites.

Although ungrazed fields can support high insect numbers (Lavigne and Kumar 1972), the height of the grass may have obscured insect visibility.

Lewis' Woodpeckers did not nest near dense tree stands, a trend noted in other studies (Bendire 1895, Bent 1939, Snow 1941, Bock 1970, Sousa 1982). Dense forest stands may impede flycatching maneuverability and, in addition, numbers and visibility of flying insects may be low. Nests did not occur near anthropogenic structures, possibly because Lewis' Woodpeckers are shy birds (Snow 1941, Bock 1970). Habitats surrounding nest sites on the plains differed from random sites ($\chi^2 = 85.7$, df = 7, $P < .001$) (Fig. 2), but patterns differed from those found in the foothills. While birds in the foothills nested near lightly grazed fields, heavily grazed fields on the plains were avoided, possibly because of low insect abundance (Lavigne and Kumar 1972). Nests occurred near fallow and mowed fields; fallow fields can support high insect numbers (Lavigne and Kumar 1972) and mowed fields may have increased insect visibility while still retaining enough plant biomass to support adequate insect populations.

In 1993, plains habitat characteristics again differed between occupied and random sites ($\chi^2 = 85.7$, df = 7, $P < .001$) (Fig. 3), but patterns were very different than in 1992. The birds avoided fallow fields, mowed fields, grazed fields, and areas with many trees. Nest sites occurred near

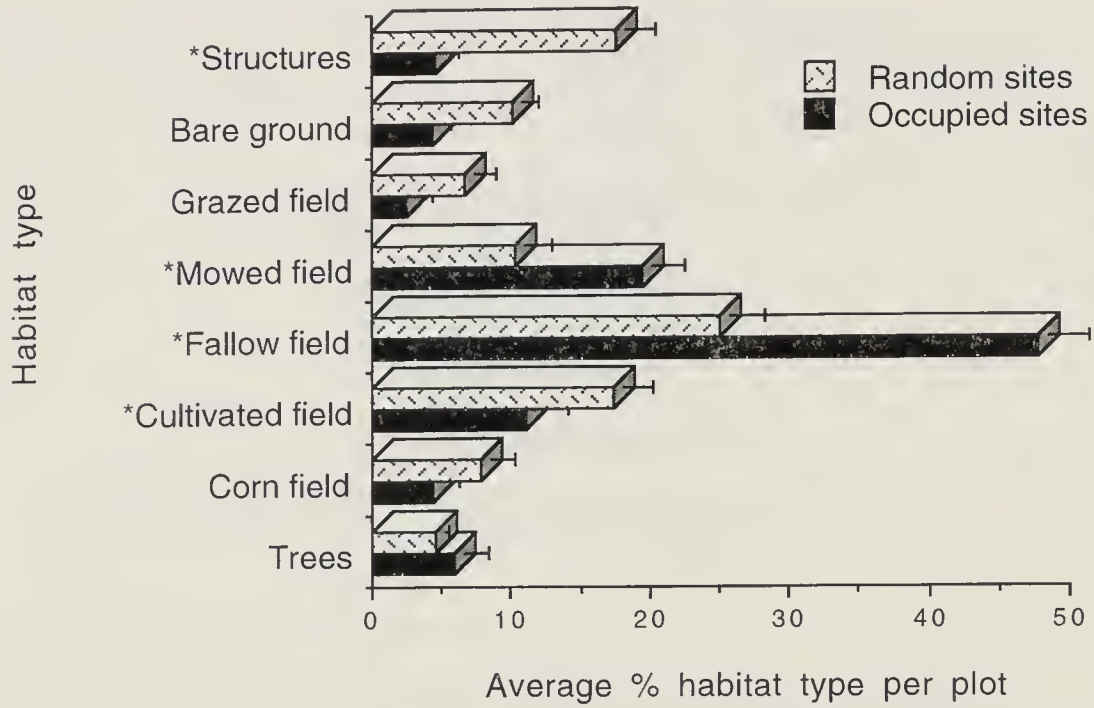

FIG. 2. Characteristics (mean percent habitat type per plot ± SD) of 100-m diameter plots surrounding 11 Lewis' Woodpecker nest trees vs 11 random trees during the 1992 breeding season on the plains of eastern Colorado. Asterisks represent those habitat variables which differ significantly between occupied and random sites.

cultivated fields, especially near corn fields. Corn fields did not occur near nest sites in 1992 but were common in 1993 breeding sites; this difference was due to many of the wintering birds remaining on their winter sites into the 1993 breeding season. Many of the birds breeding in 1992 may have also stayed on their 1991–1992 winter sites. However, by the beginning of the 1992 breeding season, many of the corn fields had been plowed and were fallow in the summer of 1992.

Winter habitat characteristics and the effects of mast on winter site selection.—Occupied winter sites in the foothills differed from random sites ($\chi^2 = 38.1$, df = 6, $P < .001$) (Fig. 4). While occupied winter sites did not occur near ungrazed fields, structures, or bare ground, they did occur near oaks. Acorn crops were higher at occupied sites than at random sites ($U = 1352$, df = 1,51, $P < .002$). An average of 28.3 ± 4.2 total acorns occurred within a 0.5 m^2 area at 13 occupied sites, and an average of 10.4 ± 3.1 total acorns occurred at 13 random sites. Acorns are the major source of food in the winter for this species in the foothills, and Lewis' Woodpeckers wintered near good sources of this mast.

While Lewis' Woodpeckers typically defend an individual storage tree containing their acorn stores (Bock 1970), some birds in the foothills shared storage trees. Specific parts of the trees were actively defended by

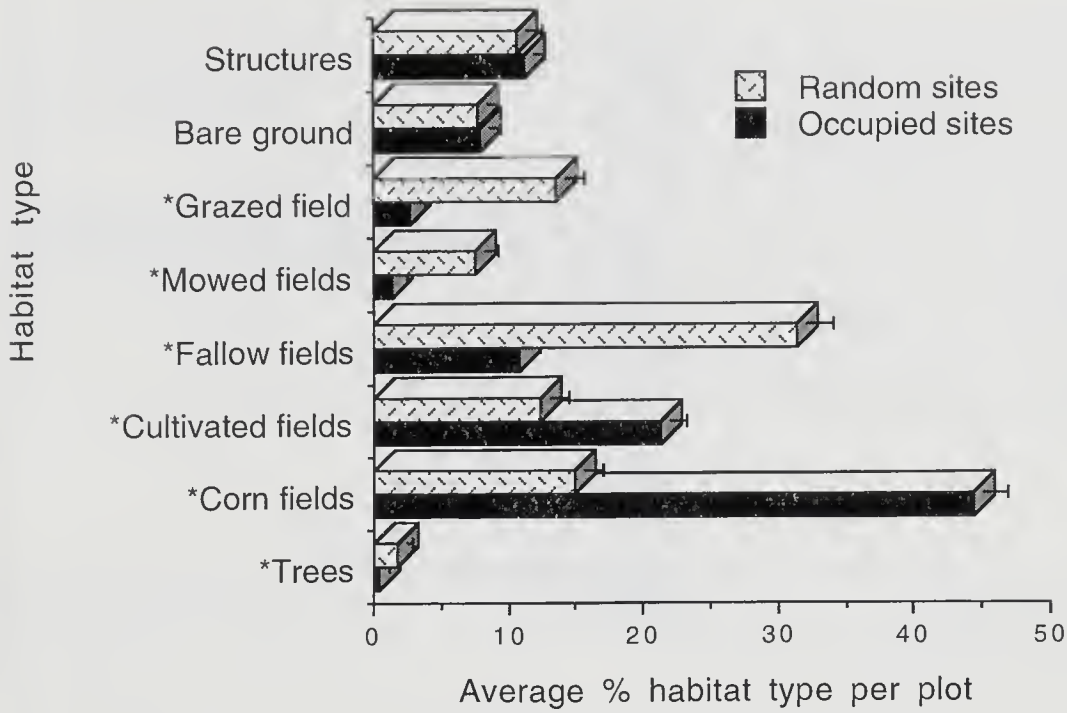

FIG. 3. Characteristics (mean percent habitat type per plot ± SD) of 100-m diameter plots surrounding 19 Lewis' Woodpecker nest trees vs 19 random trees during the 1993 breeding season on the plains of eastern Colorado. Asterisks represent those habitat variables which differ significantly between occupied and random sites.

the individuals storing acorns in that region of the tree. The sharing of storage trees in this region suggests that suitable storage trees may be a limiting resource during the winter.

Lewis' Woodpecker winter sites on the plains differed from random sites (Fig. 5) ($\chi^2 = 84.58$, df = 7, $P < .001$). Wintering birds avoided plowed, grazed, and fallow fields. Lewis' Woodpeckers would flycatch in winter if the weather was warm enough to permit insect activity (Hadow 1973), and the absence of the birds near areas of bare ground, plowed fields and grazed fields may be related to low numbers of insects in these habitats. Corn fields comprised a major part of the surrounding winter habitat, probably because corn is the only storable mast available to Lewis' Woodpeckers on the plains.

This study demonstrates the importance of both occupied tree characteristics and the surrounding habitats in the site selection by this species. Lewis' Woodpeckers occurred primarily in riparian habitats in southeastern Colorado, and they relied heavily on large mature cottonwoods for both breeding and winter activities.

Lewis' Woodpeckers also inhabit open, park-like ponderosa pine forests during the breeding season (Bock 1970, Short 1982). However, I found little evidence of breeding activities in this habitat type. Their ab-

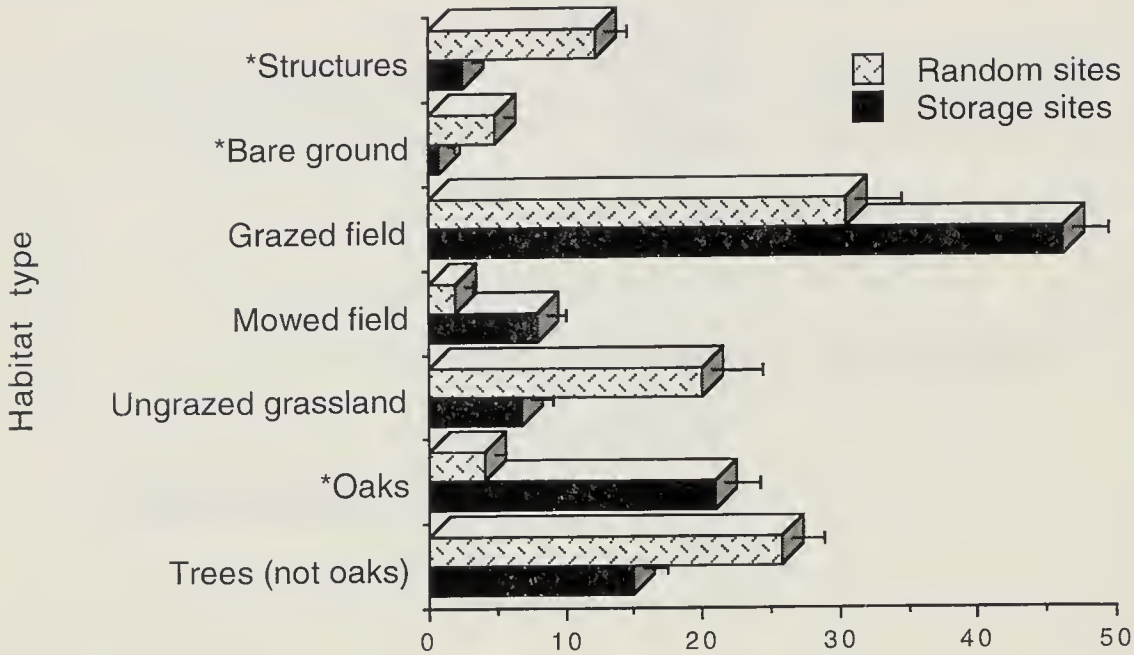

FIG. 4. Characteristics (mean percent habitat type per plot ± SD) of 100-m diameter plots surrounding 13 Lewis' Woodpecker storage trees vs 13 random trees during the 1992–1993 winter season in the foothills of the Wet Mountains. Asterisks represent those habitat variables which differ significantly between occupied and random sites.

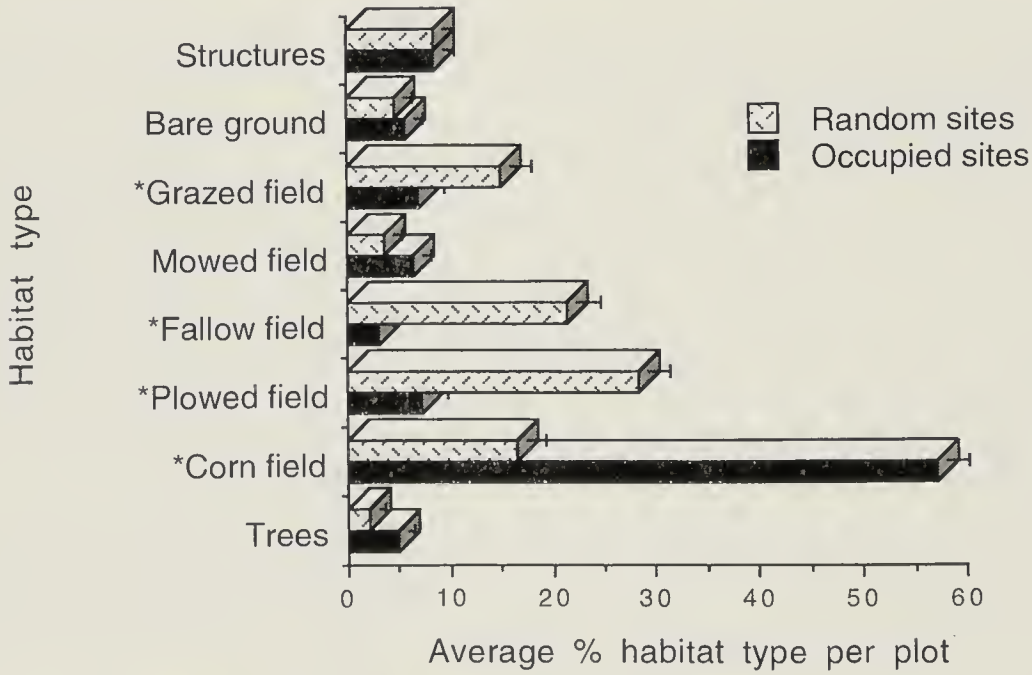

FIG. 5. Characteristics (mean percent habitat type per plot ± SD) of 100-m diameter plots surrounding 21 Lewis' Woodpecker storage trees vs 21 random trees during the 1992–1993 winter season on the plains of eastern Colorado. Asterisks represent those habitat variables which differ significantly between occupied and random sites.

sence in ponderosa pine forests may be related to the reduction of suitably open ponderosa pine forests in the region (Veblen and Lorenz 1991). These types of forests traditionally were maintained by fire and with the advent of fire suppression, ponderosa pine forests became denser (Veblen and Lorenz 1991, Covington and Moore 1994, Everett et al. 1994). Since Lewis' Woodpeckers require open areas in which to flycatch, the existing dense ponderosa pine forests in Colorado may be unsuitable for foraging purposes. Additional studies in different habitats are necessary in order to gain a comprehensive view of the habitat factors influencing site selection for breeding and wintering Lewis' Woodpeckers throughout their range.

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HOME RANGE AND HABITAT USE OF RED-SHOULDERED HAWKS IN GEORGIA

DOUG L. HOWELL[1,2] AND BRIAN R. CHAPMAN[1]

ABSTRACT.—Home range and habitat use of Red-shouldered Hawks (*Buteo lineatus*) were studied within a managed pine forest in the Georgia Piedmont during the breeding season of 1994. The average home-range size was 127.9 ± 2.4 (SD) ha for four males and 97.0 ± 12.1 (SD) ha for three females. Home-range size of three breeding pairs averaged 133.0 ± 4.5 (SD) ha. Red-shouldered Hawks were located almost exclusively within forested habitats (96% of locations). The overall pattern of habitat use for both sexes was similar. Bottomland hardwoods were used more often than expected, and upland hardwoods were used in proportion to availability at two spatial scales. Pine and non-forested habitats were used less often than expected relative to availability. Male and female core areas averaged 37% of the mean home-range size. *Received 2 Nov. 1995, accepted 20 Sept. 1996.*

Although the Red-shouldered Hawk (*Buteo lineatus*) is a widespread, permanent resident over much of the Southeast, including Georgia, no quantified information exists on its space and habitat requirements within the region. Therefore, it is difficult to predict or mitigate possible impacts of habitat alterations associated with modern, intensive production of pine timber. The objectives of this study were to establish the home range size and habitat requirements of the Red-shouldered Hawk within an intensively-managed pine forest. Silvicultural treatments associated with intensive timber management result in a wide array of forest modifications that may alter horizontal and vertical structural diversity, decrease stand diversity, or alter the size class distribution and species composition of vegetation (Nelson and Titus 1988). Such habitat alterations may affect the viability of raptor populations by influencing the availability of nest sites, habitat use, and prey abundance and vulnerability. Therefore, studies such as this may provide information useful in formulating a management plan for Red-shouldered Hawks in managed forests of the Southeast.

METHODS

Study area.—We studied Red-shouldered Hawks during the 1994 breeding season on the Bishop F. Grant Memorial Forest (BGF), in Putnam and Morgan counties, approximately 14 km north of Eatonton (33°25′W, 83°28′N), in east-central Georgia. The 5718-ha study area lies within the southern Piedmont, a region of broad, gently sloping topography with occasional steep or strongly sloping terrain around the major drainage basins (Wharton 1977). Elevation ranges from 120–220 m above sea level. Rainfall averages approximately 120 cm per year (USDA-SCS 1965, 1976), with peak precipitation occurring in winter.

[1] Daniel B. Warnell School of Forest Resources, Univ. of Georgia, Athens, Georgia 30602-2152.
[2] Present Address: Directorate of Public Works and the Environment, AFZA-PW-DW, Wildlife Branch, Ft. Bragg, North Carolina, 28307-5000.

Eighty-five percent of BGF is forested, and is managed principally for the production of pine timber by the Daniel B. Warnell School of Forest Resources at the Univ. of Georgia. Fifty-five percent of the BGF land area consists of stands of loblolly pine (*Pinus taeda*). Pine habitats are managed with both natural and artificial regeneration methods combined with thinning and prescribed burning. Pine habitats are categorized by age-class and structural characteristics, and include <6 yr (clearcut), 6–20 yr (regeneration), 21–30 yr (pulpwood), 31–50 yr (sawtimber), and >50 yr (old sawtimber) stands.

Clearcuts typically consist of pine seedlings interspersed with several species of perennial grasses, including broomsedge (*Andropogon virginicus*) and plumegrass (*Erianthus* spp.), scattered hardwood sprouts, and blackberry (*Rubus* spp.) thickets. Regenerating stands are dominated by pines, with understory vegetation suppressed by shade and pine needles. The remaining age-classes have been thinned to various degrees, and represent product classes from pulpwood to sawtimber. Understory species include sweetgum (*Liquidambar styraciflua*), flowering dogwood (*Cornus florida*), and black cherry (*Prunus serotina*). Ground cover includes broomsedge, blackberry, and muscadine (*Vitis rotundifolia*). Prescribed winter burns every 3–5 years reduce fuel loads and competition from hardwoods.

Bottomland hardwood forests (7% of area) exist along the area's major drainages; Big Indian Creek, Glady Creek, and Little River. Dominant canopy species include green ash (*Fraxinus pennsylvanicus*), sweetgum, boxelder (*Acer negundo*), river birch (*Betula nigra*), sycamore (*Platanus occidentalis*), overcup oak (*Quercus lyrata*), water oak (*Q. nigra*), and willow oak (*Q. phellos*). The understory includes red maple (*Acer rubrum*), ironwood (*Carpinus caroliniana*), and American elm (*Ulmus americana*). Possum haw (*Ilex decidua*), switch cane (*Arundinaria gigantea*), and privet (*Ligustrum sinense*) dominate the shrub layer, while microstegium (*Microstegium vimineum*) and Christmas fern (*Polystichum acrostichoides*) are the dominant ground cover.

Upland hardwood stands (23%) lie adjacent to the bottomland corridor, or are associated with the major drainage basins. Dominant canopy species include white oak (*Quercus alba*), southern red oak (*Q. falcata*), pignut hickory (*Carya glabra*), blackgum (*Nyssa sylvatica*), sweetgum, and winged elm (*Ulmus alata*). The mid-story is dominated by flowering dogwood, and the shrub layer is dominated by sparkleberry (*Vaccinium arboreum*), deerberry (*V. stamineum*), and highbush blueberry (*V. corymbosum*). Common ground cover species include muscadine and poison ivy (*Toxicodendron radicans*). The remainder of BGF is maintained as pasture (14%) for cattle grazing and hay production by the College of Agriculture at the Univ. of Georgia, or is planted as wildlife openings (1%). In addition, several small reservoirs provide irrigation water, public fishing, and waterfowl habitat.

Capture and radio-telemetry.—We captured Red-shouldered Hawks with a modified dho-ghaza (Hamerstrom 1963) with a live Red-tailed Hawk (*B. jamaicensis*) as the lure. One female hawk which did not respond to the dho-ghaza was captured with a bal-chatri trap (Berger and Mueller 1959) baited with a black rat (*Rattus rattus*). Sex and age of each hawk were determined based on the presence or absence of a brood patch, body mass, and plumage characters (Clark and Wheeler 1987).

All hawks were fitted with radio-transmitters (Telonics Inc., Mesa AZ) and banded with a U.S. Fish and Wildlife Service aluminum leg band. Transmitters had a range of 2 km, and were attached in a backpack configuration (L. Schueck, Greenfalk Consultants, pers. commun.) with tubular teflon ribbon. Each transmitter included an activity sensing "tip-switch" that resulted in the transmission of two different pulse rates, depending on the orientation of the transmitter to the ground (i.e., perched or flying). The combined mass of the transmitter and harness (18–26 g) was <5% of each hawk's body mass. Soon after release, all radio-tagged hawks resumed normal activities, and no problems associated with the radio attachment method were observed.

We determined the locations of radio-tagged hawks by triangulation with a hand-held, four-element yagi antenna and visual sightings. At least three compass bearings were taken sequentially within 15 min to determine each hawk's location. All bearings were taken from predetermined locations (stations) along the existing road system, which allowed us to minimize the distance between the receiver and a transmitter, reduce signal bounce due to topography, and maintain angles for triangulation near 90°. Bearing standard deviation was estimated by conducting field trials with transmitters in 10 known locations (White and Garrott 1990). Two-hundred test bearings were used to calculate a mean bearing error of ± 3.02°. Universal Transverse Mercator (UTM) coordinates of receiver stations and locations of test transmitters were established with a mobile global positioning system (GPS Pathfinder Basic Plus, Trimble Navigation, Sunnyvale, California), and differentially corrected to an accuracy of ± 2 m.

We located radio-tagged hawks during five periods covering their movements from morning (1 h before sunrise) to night (1 h after sunset) roosts: 06:00-08:59 h; 09:00–11:59 h; 12:00–14:59 h; 15:00–17:59 h; 18:00–21:00 h (EST). Observation periods were randomly allocated to ensure all periods were sampled with equal probability over the course of the breeding season. For this study, the breeding season was defined as that period from courtship and nest building (1 March) until the young had fledged, or had fledged but were still dependent on one or both adults (31 August). Frequently, after a hawk was located with telemetry, it was followed visually for several hours. Information on exact movement patterns and behaviors was recorded. Caution was exercised so visual monitoring of hawks had little effect on their normal activities.

Based on their frequent movements, locations of radio-tagged hawks were normally recorded at 30-min intervals. Movements were inferred from a noticeable change in transmitter signal strength and/or a change in the pulse frequency, followed by a change in signal direction. Locations were included only if the hawk was stationary as bearings were recorded. When hawks were monitored visually, each perch change >100 m was recorded as a location. Location estimates and 95% confidence ellipses for each triangulated location were calculated with maximum likelihood estimation (MLE) (Lenth 1981). The mean confidence ellipse size was 1.37 ± 0.46 (SD) ha (range = 0.1–3.5 ha). Most (79%) confidence ellipses were <1 ha. Hawk locations obtained visually (34% of locations) were recorded in the field on 7.5-minute U.S. Geological Survey topographic maps based on map landmarks and a global positioning system.

Home-range analysis.—We estimated the size and shape of Red-shouldered Hawk home ranges by the harmonic mean (HM) method (Dixon and Chapman 1980) with the computer program HOME RANGE (Ackerman et al. 1990). The contour line encompassing 95% of all locations for an individual hawk was used as the home-range boundary. Core areas were identified by comparing the observed space-use pattern (utilization distribution) of hawks with that expected from a uniform pattern of use (Samuel and Green 1988). Core areas included the maximum area where the observed utilization distribution (based on harmonic values) exceeded a uniform utilization distribution. All harmonic mean calculations were based on a grid size of 75 m. The minimum convex polygon (MCP) home range (Mohr 1947) was estimated to permit comparisons with earlier studies.

The index of autocorrelation (gamma) recommended by Swihart and Slade (1986) was used to assess the level of autocorrelation in the locational data. We assumed gamma values >0.3 indicated significant autocorrelation (Ackerman et al. 1990). We calculated the "time to independence" (Swihart and Slade 1986) for each hawk with the HOME RANGE program. For all hawks, the level of autocorrelation was reduced to an insignificant level (gamma <0.3) at a 2-h sampling interval. Therefore, only observations separated by two

hours or more were used in analyses of home range and habitat use in order to meet assumptions of independence.

Habitat-use analysis.—We developed a digital database with the geographic information system (GIS) software package ARC/INFO (ESRI 1991) to estimate the area of each habitat type within the study area, and within each hawk home range. The boundaries of habitat polygons were delineated from aerial photographs and forest cover maps, then transferred to the GIS using a digitizer. Aerial photographs, forest cover maps, and forest stand information were obtained from the Univ. of Georgia. The contour line defining the 95% HM home range and core area for each hawk was transferred from HOME RANGE to the GIS as a UTM coordinate file. Estimated locations were entered directly into the database as UTM coordinates to determine habitat characteristics at each location.

Using the GIS, we assessed potential habitat misclassification in the telemetry data (N = 1242 location points) resulting from bearing error (Howell 1995). We assumed a circle with a uniformly distributed radius corresponding to the size of the 95% MLE confidence ellipse was representative of telemetry error for each location. Confidence ellipses were overlayed with the computerized habitat availability map to determine the number of habitat types occurring within an ellipse. We assumed a confidence ellipse containing > 1 habitat type represented potential habitat misclassification.

We used Chi-square analysis (Neu et al. 1974) to test the hypothesis that hawks used habitat types in proportion to availability. When this hypothesis was rejected, Bonferroni confidence intervals (Byers et al. 1984) were used to determine which habitat types were used more or less often than expected. Because a species response to habitat variation (selection) may occur at more than one level (Johnson 1980), the number of locations within each habitat type was compared with habitat availability at two spatial scales: (1) within each individual hawk home range, and (2) among all hawks within the study area (landscape level). At the landscape level, available habitat was estimated from the combined 95% HM contour for all hawks. A Chi-square test was also performed to compare the proportional distribution of habitats within hawk home ranges to that expected by relative availability within a broader landscape, represented by the study area boundary. To assure a reasonable approximation to the Chi-square distribution, the 20–30 yr (pulpwood) and 31–50 yr (sawtimber) stands were pooled into a 21–50 yr pulpwood/sawtimber stand class (Neu et al. 1974). The significance level was set at 0.05 in all tests.

RESULTS

Radio-telemetry.—We radio-tracked five male and two female Red-shouldered Hawks between 14 April and 22 August 1994. Monitoring periods ranged from 59 to 102 days (average 88), totaling 656 hours of continuous observation. Removal of location points to reduce autocorrelation resulted in 1870 useable location points (Table 1). Except for one male, all hawks were territorial breeding adults. Both members of two breeding pairs (F170-M090, F190-M010) were tracked simultaneously for ≥95 days (see Table 1 for hawk codes). An adult female (F210) was observed, but not radio-tagged, for 76 days; she nested successfully with M030. There were sufficient locations to estimate the size and shape of her home range, but F210 was excluded from analysis of habitat use.

Male home-range size.—The 95% HM home range of four male Red-shouldered Hawks averaged 127.9 ± 2.4 (SD) ha (range = 126.1–131.5

TABLE 1

HOME-RANGE SIZE (HA) OF EIGHT RESIDENT RED-SHOULDERED HAWKS IN THE GEORGIA PIEDMONT, APRIL–AUGUST 1994

Hawk[a]	No. locations	Days monitored	Harmonic mean		Convex polygon	
			Core area (%)[b]	95%	95%[c]	100%
M010	316	96	50.5 (60)	131.5	154.9	301.3
M030	312	94	48.6 (62)	126.1	151.7	198.5
M050	337	82	51.6 (60)	127.3	131.5	168.3
M070[d]	168	59	—	3069.6	3133.9	3297.2
M090	312	94	58.0 (61)	126.7	143.9	163.0
F170	285	102	50.0 (65)	108.8	108.9	160.3
F190	308	95	40.4 (62)	97.6	87.5	135.5
F210	127	79	32.6 (61)	84.6	91.3	114.8

[a] M = male, F = female. Includes 3 breeding pairs (F170-M090, F190-M010, M030-F210).
[b] (%) = percent of utilization volume.
[c] Excludes outer 5% of location estimates.
[d] Subadult hawk that was a non-territorial "floater."

ha; Table 1). One subadult male (M070) was excluded from analysis because he failed to maintain a home range in the traditional sense. Although his movements seemed to center around a small riparian corridor, M070 was tracked within the home range of three other pairs, and his movements were erratic. His 95% HM home range was 24 times larger than the mean home-range size of other males (Table 1). Male home ranges were on average, 24% larger than females (range = 13.7–35.7%), and when considering only breeding pairs, generally encompassed those of their mates (Fig 1).

Although males ranged widely, all their home ranges included areas that received concentrated use. These core areas averaged 52.2 ± 4.0 (SD) ha (range = 48.6–58.0 ha; Table 1), representing only 37% (range = 34.4–43.6%) of the average male home range. All male core areas contained the nest site, but were most often centered around a small beaver (*Castor canadensis*) pond, wet meadow, or an area containing many small seasonally or permanently flooded pools. On average, approximately 61% (range = 59.6–62.0%) of male locations fell within the core area, based on harmonic mean estimates (Table 1).

Female home-range size.—The 95% HM home range of three female Red-shouldered Hawks averaged 97.0 ± 12.1 (SD) ha (range = 84.6–108.8 ha; Table 1). Female home-range size varied over the course of the breeding season. Home-range size was smallest during incubation, averaging only 30 ± 7.8 (SD) ha, but increased through brood-rearing as females foraged over wider areas. For example, during the incubation

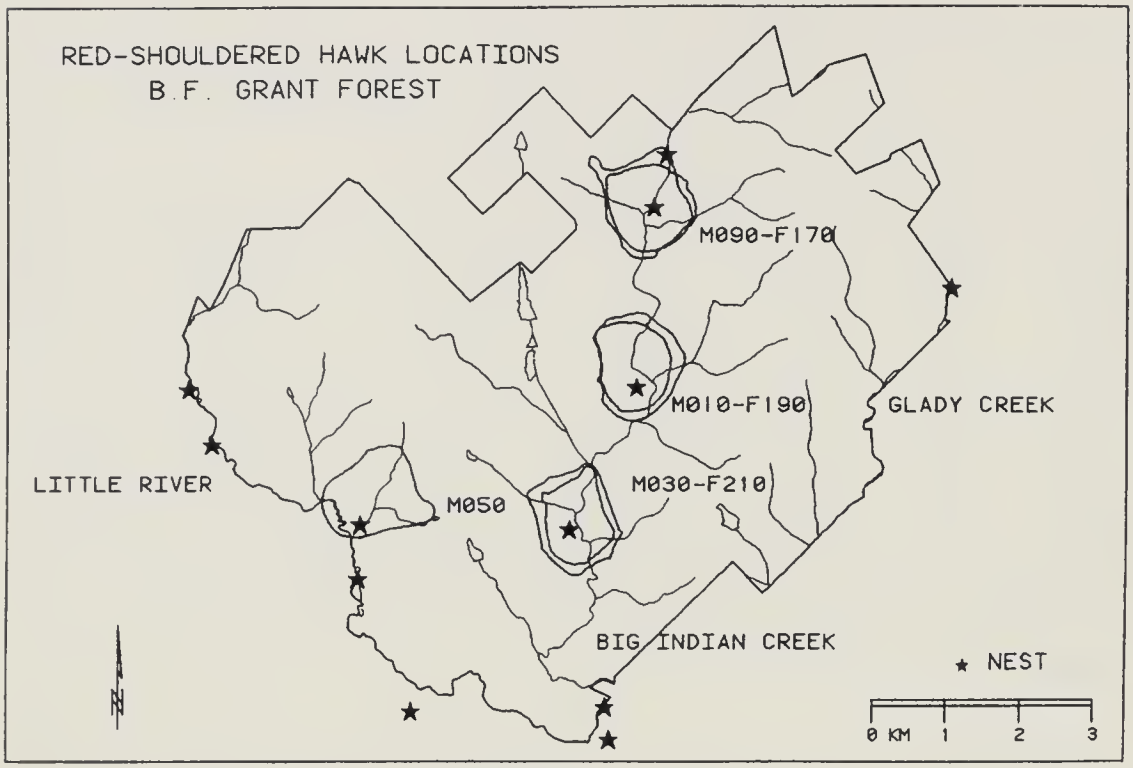

FIG. 1. Map of the Red-shouldered Hawks known to occupy the area within and adjacent to the Bishop F. Grant Memorial Forest; includes the home ranges of three breeding pairs (M090-F170; M010-F190; M030-F210) and an adult male (M050) followed April–August, 1994.

period, F170 rarely moved from the vicinity of her nest, but began making regular visits to a small beaver pond shortly after the first chick appeared.

Female core areas averaged 41.0 ± 8.7 (SD) ha (range = 32.6–50.0 ha; Table 1), representing only 37% (range = 35.2–40.5%) of the average female home range. Female core areas were centered on the nest and included intensively-used foraging sites. On average, 63% (range = 61.8–65.2%) of female locations fell within the core area (Table 1). Female core areas averaged 21% (range = 0–43.7%) smaller than those of males.

Pair home-range size.—The three breeding pairs of Red-shouldered Hawks (see Table 1) occupied adjacent home ranges along the Big Indian Creek corridor, which bisected BGF (Fig. 1). The combined 95% HM home range of breeding pairs averaged 133.0 ± 4.5 (SD) ha (range = 132.1–134.3 ha). Approximately 75% of a pair's home range was used by both members, while the remaining 25% was used only by the male. Areas of overlap generally encompassed both the male and female core areas. There was no overlap between home ranges of either member of adjacent pairs, and no intraspecific territorial encounters were observed.

Habitat composition within home ranges.—Forested habitats comprised

more than 91% of Red-shouldered Hawk home ranges (excluding M070, F210; Table 2). Of the forested habitats, bottomland (32.1%) and upland (21.4%) hardwoods were the most common. Stands of old sawtimber, regeneration, and pulpwood/sawtimber represented 19.6%, 16.3%, and 2.2% of home ranges, respectively. The non-forested habitats, pasture (4.5%) and clearcut (3.9%), were relatively rare in hawk home ranges. Approximately 77% and 78% of male and female core areas, respectively, consisted of bottomland and upland hardwoods.

Habitat-use patterns within home ranges.—Chi-square tests of habitat selection within home ranges were significant ($P < 0.001$) for all hawks (N = 6) available for analysis (Table 3). All hawks used bottomland hardwoods more often than expected, while use of upland hardwoods was proportionate to area (Bonferonni Z-test, $P < 0.05$). In general, non-forested habitats, regeneration, and pulpwood/sawtimber were not present within home ranges, not used, or used less often than expected relative to availability; old sawtimber was used in proportion to availability, or less often than expected.

Habitat-use patterns within study area.—Habitat use within the study area was not random. For both males and females, the observed number of radio locations differed from expected, based on the area of each habitat type within home ranges (males–χ^2 = 481, df = 6, $P < 0.001$; females–χ^2 = 146.8, df = 6, $P < 0.001$) (Table 3). The overall pattern of habitat use for both sexes was similar (Bonferonni Z-test, $P < 0.05$). Both males and females used bottomland hardwoods more often than expected, based on its availability, while use of upland hardwoods was approximately proportionate to area. Most (78%) locations were in bottomland (56.9%; males, 693 of 1277; females, 371 of 593) and upland hardwoods (21.0%; males, 300 of 1277; females, 93 of 593), respectively (Table 2). Regeneration, pulpwood/sawtimber, and old sawtimber stands were used less often than expected, representing 17.8% of the observed habitat use (males, 178 of 1277; females, 74 of 593 locations). Red-shouldered Hawks used non-forested habitats less often than expected based on availability. Collectively, pasture and clearcut represented only 4.3% of observed habitat use (males, 72 of 1277; females, 46 of 593 locations), but make up (18%) of the area.

The distribution of habitat types within hawk home ranges (N = 6) differed from expected based on their relative availability within BGF (χ^2 = 98, df = 6, $P < 0.001$). Overall, home ranges contained more bottomland forests, while the proportion of upland hardwoods was equal to availability (Bonferonni Z-test, $P < 0.05$). In addition, home ranges contained less pasture, clearcut, and old sawtimber, while the proportions of regen-

TABLE 2

PERCENTAGE OF DIFFERENT HABITATS WITHIN THE 95% HARMONIC MEAN HOME RANGE AND PERCENTAGE OF ESTIMATED LOCATIONS WITHIN DIFFERENT HABITATS

	Hawk number													
	M010		M030		M050		M090		F170		F190		All hawks	
Habitat[a]	Hab.	Loc.	Hab.	Loc.	Hab.	Loc.	Hab.	Loc.	Hab.	Loc.	Hab.	Loc.	Hab.	Loc.
BLHW	42.8	66.8	19.6	46.6	23.0	55.8	30.6	47.7	29.2	49.2	50.8	75.0	32.1	56.9
UPHW	18.1	15.8	29.6	28.0	20.2	23.7	23.6	26.6	21.4	21.5	14.2	10.4	21.4	21.0
PAST	6.2	4.1	10.6	5.5	1.9	+	1.2	+	1.4	+	5.3	2.6	4.5	2.3
C-CUT			7.3	7.4			8.4	2.9	7.6	2.1			3.9	2.0
REGEN	18.5	5.4	23.6	2.9	14.7	+	10.7	3.5	11.6	7.4	18.6	6.2	16.3	4.3
21–50 YR	1.1	+					6.7	3.2	4.0	1.8	1.2	+	2.2	1.1
>50 YR	13.3	7.3	9.3	9.6	40.2	19.0	18.8	15.4	24.8	17.9	9.9	5.2	19.6	12.4

[a] Habitat codes: BLHW = bottomland hardwood; UPHW = upland hardwood; PAST = pasture; C-CUT = clearcut; REGEN = regeneration; 21–50 YR = pulpwood/sawtimber; >50 YR = old sawtimber; + = <1%; N = 1870 locations.

TABLE 3

HABITAT SELECTION BY SIX RED-SHOULDERED HAWKS IN THE GEORGIA PIEDMONT, APRIL–AUGUST 1994[a]

	Hawk[b]						All hawks[c]	
Habitat	M010	M030	M050	M090	F170	F190	M	F
BLHW	+1	+1	+1	+1	+1	+1	+1	+1
UPHW	0	0	0	0	0	0	0	0
PAST	0	−1	NU	NU	−1	−1	−1	−1
C-CUT	NP	0	NP	−1	−1	NP	−1	−1
REGEN	−1	−1	NU	−1	−1	−1	−1	−1
21–50 YR	NU	NP	NP	−1	−1	NU	−1	−1
>50 YR	−1	0	−1	0	−1	−1	−1	−1

[a] Selection evaluated using chi-square tests with Bonferonni confidence intervals (Neu et al. 1974); 0 = use of habitat equal to expected; −1 = use of habitat less than expected; +1 = use of habitat greater than expected; NU = not used; NP = not present within home range.
[b] Available habitat sampled from individual 95% HM home range.
[c] Available habitat sampled from combined 95% HM contour.

eration and pulpwood/sawtimber were equal to their relative availability within the study area.

Habitat misclassification.—Potential habitat misclassification due to bearing error had little effect on the habitat-use analyses. Eighty-seven percent of the MLE confidence ellipses (N = 1242) contained only one habitat type (Howell 1995). Sixty-six percent of potential misclassification (107 of 162 locations) represented a confidence ellipse containing bottomland (28%) or upland hardwoods (38%). Most (45%) of the potential misclassification represented a bottomland hardwood/upland hardwood or upland hardwood/bottomland hardwood misclassification matrix and reflected the heavy use of the bottomland—upland ecotone.

DISCUSSION

Home range.—Home-range estimates for Red-shouldered Hawks on BGF support previous findings that suggest the species uses the smallest home range of any North American buteonine raptor studied to date. Parker (1986) reported a mean MCP of 118 ± 13 ha for two males in Missouri, an estimate similar to this study (mean MCP = 145 ± 10 ha, N = 4 males). In an intensive study of the western subspecies (*B. l. elegans*), Bloom et al. (1993) found the mean home range (95% HM) of seven males was 121 ± 35 ha, and six females was 101 ± 19 ha, similar to the home-range size of males (128 ± 2 ha) and females (97 ± 12 ha) reported here.

The location and shape of home ranges were influenced by the topographic characteristics of the bottomland habitats within the study area.

Almost all home ranges were found within the widest portions of the bottomland corridor, normally in areas fed by one or more perennial streams. These areas held seasonal floodwaters and precipitation as temporary or permanent pools, contained beaver ponds, and likely provided a diverse and abundant source of prey. Sixty percent of the prey delivered to eight Red-shouldered Hawk nests on BGF (Howell 1995) were those associated with or found only in aquatic or moist habitats. Red-shouldered Hawk core areas generally conformed to the distribution of the temporary or permanent pools and small open wetlands (≤1 ha) within the home range.

Home ranges of Red-shouldered Hawks on BGF were rather evenly distributed along the bottomland corridor of the areas three main waterways (Fig 1). The nests of 12 pairs that occupied BGF were generally separated by approximately 2 km. Stewart (1949) and Henny et al. (1973) noted that Red-shouldered Hawks occupied evenly distributed home ranges along floodplain forest corridors in Maryland. Newton (1979) suggested that in continuously suitable habitat, nesting pairs of raptors are often separated by roughly equal distances, thus reducing interference in breeding and hunting.

The three breeding pairs of Red-shouldered Hawks that we tracked occupied mutually exclusive home ranges (Fig. 1). Bloom et al. (1993) reported an overlap of only 5% between adjacent home ranges of three breeding pairs in California. In both instances where adjacent nests were located <1 km apart, one of the two pairs either abandoned the nest or failed to produce young (D. L. Howell and C. E. Moorman, pers. obs.). Henny et al. (1973) found that as the distance between adjacent Red-shouldered Hawk nests decreased, nesting success decreased, and concluded nest success was inversely proportional to the number of breeding pairs present.

Habitat use.—Red-shouldered Hawks on BGF hunted almost exclusively within forested habitats, employing still-hunting from perches as the primary foraging method. Bednarz and Dinsmore (1981), Parker (1986), and Bloom et al. (1993) showed similar trends of preference for forested habitats by Red-shouldered Hawks. Bloom et al. (1993) suggested that Red-shouldered Hawks in California were limited in their use of non-forested habitats by the availability of perches. On BGF, both pastures and clearcuts contained ample perches from which hunting attempts could be initiated. However, these open habitats were also favored habitats of resident Red-tailed Hawks (Moorman and Chapman 1996), which may have deterred use by Red-shouldered Hawks. Red-tailed and Red-shouldered hawks usually maintain mutually exclusive feeding territories in North America (Bent 1937, Craighead and Craighead 1956).

Among the forested habitats, pine stands represented only about 18% of the observed habitat use. The limited use of regeneration areas was not surprising. These were densely stocked (approximately 3600 stems/ha) stands with closed canopies, which generally hold little prey value for raptors until thinning resumes (Langley and Shure 1980). Here, Red-shouldered Hawks normally concentrated their foraging efforts along old fire-breaks, which had regrown to perennial grasses and could be hunted from perched positions along an adjacent woodland edge, normally a bottomland or upland hardwood corridor.

The overall use of pine habitats was linked to the age and structure of the stands. Red-shouldered Hawks rarely used young pulpwood stands that had received only one thinning (Tables 2 and 3). Use was greatest within old sawtimber stands that had received at least two thinnings, or were present as shelterwood regeneration and where regular prescribed burning had created a open understory (Table 2). This may be a reflection of prey abundance, and the ability of a hawk to detect and capture prey in more open forests.. King (1982) found that both numbers and biomass of small mammals were greater in mature loblolly pine stands (i.e., a mean age of 57 yr) with a regular burning regime (1–4 yr) than in only thinned or unmanaged stands. Pulpwood stands were densely stocked (1200 stems/ha), and may have limited a hawk's maneuverability relative to older, more open stands. In addition, the hardwood understory in these stands had not been removed by winter burns, which may have limited hawks' ability to detect and capture prey. Studies of Swainson's Hawks (*B. swainsoni*) and Ferruginous Hawks *(B. regalis)* found vegetative cover limited access to prey, and influenced hawk selection of foraging sites (Wakeley 1978, Bechard 1982).

Although Red-shouldered Hawks foraged widely, they tended to remain within bottomland hardwoods, concentrating their hunting efforts within relatively small portions of their home range. The use of upland hardwoods was restricted to areas immediately adjacent to the bottomland corridor, or along the drainage of small perennial streams that flowed into a major water-course. Hawks would often position themselves to hunt the ecotone between the two habitats. Similar habitat use by Red-shouldered Hawks was noted in Iowa (Bednarz and Dinsmore 1981) and California (Bloom et al. 1993).

The Red-shouldered Hawk's association with forested wetland habitats is well-documented (Bednarz and Dinsmore 1981, 1982), but characteristics of its home range and habitat use within an intensively-managed forest in the Southeast were previously undescribed. The pattern of habitat selection for bottomland hardwoods relative to other habitats was identical when available habitats were sampled from the study area (second-order

selection, Johnson 1980), or from within individual home ranges (third-order selection), suggesting this habitat may be a limiting factor on BGF. We suggest that 133 ha of mature bottomland forest, interspersed with seasonally or permanently flooded pools and small open wetlands (≤1 ha) provides adequate space and habitat for one pair of Red-shouldered Hawks if adequate prey densities are also available.

Areas of upland hardwoods adjacent to the bottomland corridor should be maintained in a managed forest as buffer habitats. These areas can provide food when prey availability is low within the bottomland forest, and can limit competition from Red-tailed Hawks. Bednarz and Dinsmore (1981) found that upland forests may compensate for limited floodplain forest around some Red-shouldered Hawk nests in Iowa, and may discourage competition from Red-tailed Hawks, a species adapted to more open habitats. Forest clearing and development of pastures along drainage systems shifts the competitive advantage from Red-shouldered to Red-tailed Hawks in bottomland forests (Bednarz and Dinsmore 1982). Where intensive management for pine timber results in the reduction of bottomland forests to narrow corridors or streamside management zones surrounded by young pine plantations, the habitat available to Red-shouldered Hawks becomes less suitable, and thus may accelerate incursion by Red-tailed hawks.

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NESTLING PROVISIONING BY THE EXTREMELY DICHROMATIC NORTHERN CARDINAL

TAMATHA S. FILLIATER[1] AND RANDALL BREITWISCH[1,2]

ABSTRACT.—We measured feeding rates of nestlings during 143 h of observation on 23 pairs of the extremely dichromatic and socially monogamous Northern Cardinal (*Cardinalis cardinalis*). Males fed at higher rates than did females, both when measured as rate per brood and as rate per nestling. Only males maintained their feeding rate per nestling with an increase in brood size and increased their feeding effort as nestlings aged. Feeding efforts by mates were correlated, even when controlling for the effects of brood size. These results provide support both for hypotheses predicting substantial male parental effort in socially monogamous birds and for the assortative mating hypothesis, predicting that birds of similar quality mate with one another. We reject the deflection hypothesis predicting low paternal provisioning effort in strongly dichromatic species and conclude that any cost to male cardinal ornamentation is not simply related to male activity at the nest. *Received 26 Jan. 1996, accepted 10 Sept. 1996.*

Socially monogamous, biparental passerines expend considerable parental effort in provisioning altricial nestlings and fledglings (Skutch 1976, Breitwisch 1989, Zaias and Breitwisch 1989, Clutton-Brock 1991). Although this effort potentially is costly to parents, our knowledge of the relative efforts expended by the sexes during parental care is incomplete. Verner and Willson (1969) concluded that in all socially monogamous North American passerines sampled, males feed both nestlings and fledglings. Their samples of dimorphic species included 42 species (nestling data) and 10 species (fledging data) in which "dimorphic" pertained either to size or plumage sexual dimorphism. However, whether the relative paternal effort in provisioning differs with increasing dichromatism in socially monogamous species is unknown. We simply do not have data from enough species along the spectrum of dichromatism to make this comparison.

Northern Cardinals (*Cardinalis cardinalis*) are strongly dichromatic (Rohwer et al. 1980). Males are scarlet red and females are brown. Both sexes have orange-red bills, and there is variation in plumage and bill color among individuals of both sexes. It is very probable that such distinctive and/or conspicuous coloration is the product of sexual selection (Butcher and Rohwer 1989). Both males and females are involved in raising offspring, especially in provisioning nestlings and fledglings (Laskey 1944, Bent 1968, RB and TSF, pers. obs.).

Cardinals are socially monogamous, and although Ritchison et al.

[1] Dept. of Biology, Univ. of Dayton, Dayton, Ohio 45469-2320.
[2] Corresponding author.

(1994) have recently found that extrapair fertilizations occur in a northern Kentucky population, the 14% incidence is relatively low for a socially monogamous passerine. They suggested that this low incidence may be a function of significant male parental effort. Although they knew from their own observations that male feeding effort may be substantial, they presented no data on this effort.

We studied parental feeding of nestling Northern Cardinals to determine the effort by males and females in feeding nestlings and to thereby provide information pertinent to the question of relative parental investment by the sexes. Because parental investment contains a variety of components (Trivers 1972, Breitwisch 1989), the relative rate of provisioning by the sexes cannot, in general, be predicted by parental investment hypotheses (Clutton-Brock 1991). Nonetheless, as the primary behavioral component of parental investment, provisioning effort is of interest in itself.

In addition, two hypotheses do indeed predict relative levels of provisioning. The "deflection" hypothesis (Cott 1964, Baker and Parker 1979) assumes that in dichromatic species the activity of brightly plumaged males near the nest is costly in terms of increasing nest conspicuousness to visually orienting predators and, therefore, predicts that female provisioning exceeds male provisioning. The "skewed sex ratio" hypothesis (Breitwisch 1989) assumes that commonly occurring male-biased sex ratios in birds arise from causes other than parental investment. It predicts that in species with male-biased adult sex ratios, male provisioning exceeds female provisioning because females as a limiting resource demand high parental investment by their mates under the threat of "divorce." For most species, provisioning is the component of care that males can most readily increase.

Finally, the assortative mating hypothesis predicts that birds will mate with individuals of similar quality (Burley 1981, 1983, Breitwisch 1988). For the focus of this study, it predicts that feeding efforts by mates will be correlated, once controlling for the effects of brood size.

STUDY AREA AND METHODS

We conducted this study at the Aullwood Audubon Center and Farm located ca 15 km northwest of Dayton, Ohio (39°52′N and 84°16′W) from April to August 1991 and 1992. The Aullwood property is an 80 ha sanctuary with a variety of habitats from secondary forest and open woodlands to meadows and prairies (see Filliater-Lee [1992] for further details on vegetation). This mixture of habitats is ideal for Northern Cardinals, and they are abundant on the property, frequently on contiguous territories.

We measured nestling feeding rates of males and females in 23 pairs by recording the number of feeding trips by each parent during 1-h sampling periods (N = 143 h). In 20 of 23 cases, we knew the brood size and could standardize feeding rates as feedings per nestling

per hour. In three cases where brood size was unknown, we assumed the modal brood size for the population of two nestlings. This assumption is unbiased insofar as dispersion around this value is essentially symmetrical in this population (see Results). We report feeding rates both as overall rates and as rates per nestling. The former reflects the total effort made by each parent, while the latter allows comparison of parental efforts from the standpoint of an individual nestling.

We made all observations from distances of at least 5 m, usually partially hidden by vegetation to avoid disturbing parent birds. We recorded feeding data during at least 4 h of observations on each pair ($\bar{x}$ = 6.2 ± 1.5 h, N = 23), with sampling periods scattered throughout daylight hours (07:00–19:00 EST) and on several days distributed over the 10-d nestling period. The sampling protocol represented a compromise between attempting to sample as many pairs as possible and achieving a reasonable sample of observations for each pair. Filliater-Lee (1992) demonstrated that neither male nor female feeding effort is related to time of day. Sampling distribution with respect to mean age of nestlings was similar for broods of different sizes (Kruskal-Wallis one-way ANOVA, $H = 2.91$, df = 3, $P > 0.05$). No data were collected during rainy periods because rainfall may affect female feeding rate by extending brooding time (Johnson and Best 1982).

Cardinals carry food to nestlings deep in their bills, and food items only occasionally projected beyond the margins of the bill (e.g., caterpillars). Therefore, it was not possible to estimate by observation the relative load sizes delivered to nestlings. Although we attempted to sample foods through the use of pipe cleaner collars, we found that the bolus of mashed food items slid past the point of constriction on the nestling's throat. Mobley (1993) has shown that male cardinals provision nestlings with larger food loads than do females, and we conservatively assume that male loads are at least as large as female loads. It has similarly been shown for other passerines that males tend to bring similar-sized or larger food loads to nestlings than do females (Wittenberger 1982, Breitwisch et al. 1986, Carlson and Moreno 1986, Grundel 1987).

The sample sizes in analyses are the numbers of pairs of cardinals. Analyses employed non-parametric tests (one exception; see below) due to moderately-sized samples and unknown underlying distributions of variables (Siegel and Castellan 1988). We used the Wilcoxon matched-pairs signed-ranks test (smaller W value reported) in comparing male and female feeding rates within pairs. We used tests of independence to ask if differences in distributions of variables occurred between years; all were corrected due to small sample sizes using Williams' correction (Sokal and Rohlf 1995). We tested for monotonic relationships with Spearman rank correlations (r_s value reported), and all correlation coefficients were corrected for ties. To determine if mates display similar feeding rates, we employed a Kendall partial rank correlation ($T_{xy.z}$ value reported). First, we calculated three Kendall rank correlation coefficients (corrected for ties): (1) male feeding rate/nestling correlated with brood size, (2) female feeding rate/nestling correlated with brood size, and (3) male and female feeding rates correlated with one another (T value reported). Then, we used these to compute the partial rank correlation coefficient for feeding rates by mates that controls for the effect of brood size on individual feeding rates (Siegel and Castellan 1988). We employed the parametric F-test for the comparison of variability in feeding rates among males and females. Tests related to questions of male-female differences were two-tailed. Tests of questions relating provisioning to brood size and age were one-tailed because the predicted relationship to these variables is unidirectional. We report results as significant if associated with an *alpha* value of $P < 0.05$.

We pooled data from the two years of the study for analysis after testing for differences in the distributions of variables between years. Tests of independence revealed no differences between years in either feeding rates or brood sizes (all Ps > 0.05). For unbanded pairs,

TABLE 1

FEEDING RATES BY MALE AND FEMALE NORTHERN CARDINALS AND MALE PROPORTION OF TOTAL FEEDING EFFORT AS A FUNCTION OF BROOD SIZE

	Feedings/nestling/h		Feedings/h		
Brood	Male ($\bar{x}$ ± SE)	Female ($\bar{x}$ ± SE)	Male ($\bar{x}$ ± SE)	Female ($\bar{x}$ ± SE)	Male proportion
1 (6)[a]	1.51 ± 0.18	1.04 ± 0.12	1.51 ± 0.18	1.04 ± 0.12	0.59
2 (10)	1.08 ± 0.16	0.89 ± 0.15	2.16 ± 1.04	1.78 ± 0.31	0.55
3–4 (7)	0.94 ± 0.21	0.71 ± 0.21	3.06 ± 0.78	2.24 ± 0.25	0.58
Total (23)	1.14 ± 0.11	0.87 ± 0.08	2.30 ± 0.31	1.76 ± 0.18	0.57

[a] Number of pairs in parentheses.

we think it unlikely that a pair was sampled twice because we sampled from different territories in the two years, and it is known that pairs maintain the same territory in successive years (RB, unpubl. data).

RESULTS

Cardinals provided few feedings per hour to their broods, typically a total per pair of 2–3 feedings for broods of one nestling up to 5–6 feedings for broods of three or four nestlings (Table 1). Through binoculars, we could see that items varied from single large caterpillars to loads of many small items mashed into pulp.

Males fed nestlings at higher rates than did their mates. For total feeding rates, males surpassed their mates, averaging 2.30 ± 0.31 (SE) feedings/h, while females provided 1.76 ± 0.18 feedings/h (W = 63.5, N = 23 [with one pair tied], $P < 0.05$). Mean feeding rate per nestling by males was 1.14 ± 0.11 and by females was 0.87 ± 0.08 feedings/nestling/h (W = 57.5, N = 23 [with one pair tied], $P < 0.05$) (Table 1). The proportion of the total feeding effort provided by males was related neither to brood size ($r_s = -0.06$, N = 23 pairs, $P > 0.05$) nor to the magnitude of the total effort by the pair ($r_s = 0.18$, N = 23 pairs, $P > 0.05$) The male's proportion of total effort was as low as 0.33 and as high as 0.76 (see Fig. 1). The variance among males in mean overall feeding rate was greater than the variance among females ($F_{22,22} = 2.75$, $P < 0.05$). On a per-nestling basis, the variance in male feeding rate tended to be greater than the variance among females, but not significantly so ($F_{22,22} = 2.16$, $P = 0.08$).

Brood sizes ranged from one to four (six broods of 1 nestling, 10 broods of 2, six broods of 3, and one brood of 4). Both males and females increased their total feeding rate with brood size (for males, $r_s = 0.36$, one-tailed $P < 0.05$, N = 23; for females, $r_s = 0.52$, one-tailed $P < 0.01$,

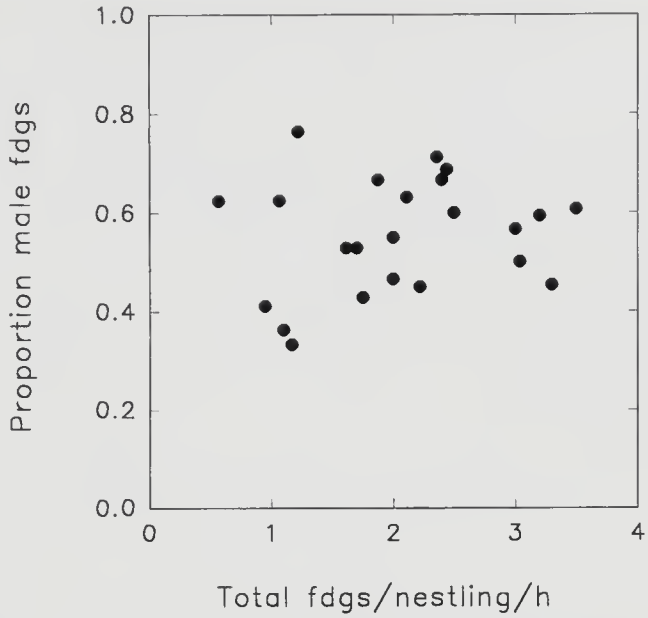

FIG. 1. Proportion of nestling feedings contributed by male Northern Cardinals as a function of total feeding effort. Data represent 23 pairs of cardinals.

N = 23). On a per nestling basis, although both sexes reduced feeding rates to larger broods, the reduction was significant only for females (for males, $r_s = -0.34$, one-tailed $P > 0.05$, N = 23; for females, $r_s = -0.47$, one-tailed $P < 0.05$, N = 23). From the standpoint of an individual nestling, the overall result was a decrease in feeding rate as brood size increased ($r_s = -0.46$, N = 23, $P < 0.05$) (Table 1).

Both males and females increased feeding effort as nestlings aged, but only males significantly did so (for males, $r_s = 0.93$, one-tailed $P < 0.01$, N = 8 days [days 0 and 1 pooled and days 8 and 9 pooled, due to small sample sizes]; for females, $r_s = 0.57$, one-tailed $P > 0.05$, N = 8 days; Fig. 2). Although not significant, the gap between feeding rates by males and females was greatest in the mid-nestling period, when altricial nestlings grow most rapidly. Females did increase their feeding rate in the four days prior to fledging.

Feeding rates by mates were correlated ($T = 0.42$, N = 23 pairs, $P < 0.01$); broods in which nestlings were fed at relatively high rates per nestling were characterized by both mates expending such high effort (Fig. 3). This was probably due in part to a brood size effect (see above). However, once we controlled for brood size, there remained a significant correlation between per-nestling feeding rates of mates ($T_{xy.z} = 0.35$, $P < 0.05$).

DISCUSSION

Male cardinals surpassed their mates in effort in feeding nestlings, better maintained their feeding rates to individual nestlings even in large

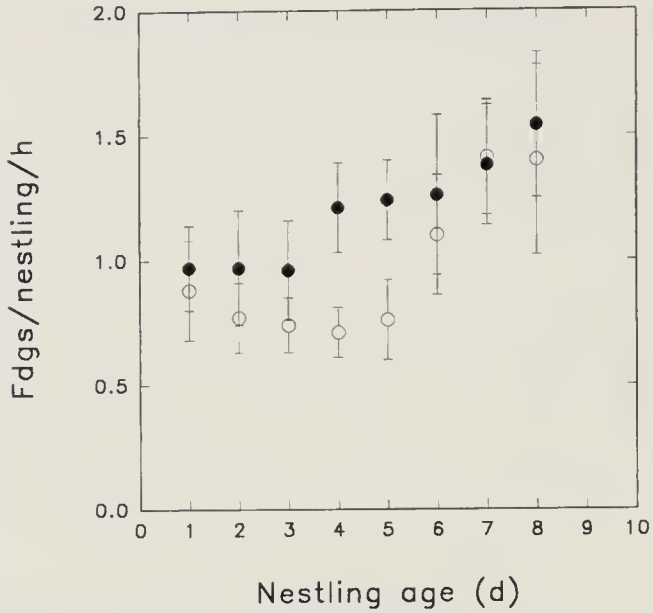

FIG. 2. Male and female Northern Cardinal nestling feeding rates as a function of nestling age. Shown are means and standard errors for each parental sex. Mean sample size (number of pairs) for each day was 13.6 ± 3.5 (range: 8–18). Males = closed circles, and females = open circles.

broods than did their mates, and tracked the growth of nestlings by consistently increasing their feeding rate as nestlings aged. These results are consistent with a prediction of the skewed sex-ratio hypothesis: males should expend the greater parental effort when they are forced to do so

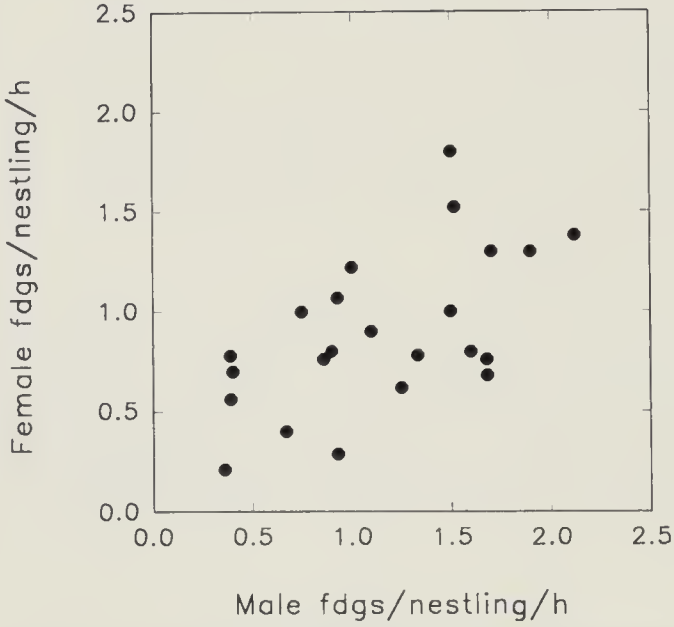

FIG. 3. Male and female Northern Cardinal mean feeding rates to nestlings standardized on a per nestling basis. Data represent 23 pairs of cardinals.

by "demands" of scarce females (Breitwisch 1989). A necessary condition for the hypothesis is that males display significant variability in their parental effort, which is the case here. Further, the difference among males is not simply related to brood size; rather, it is patternless individual variability. Unfortunately, we cannot directly address the skewed sex ratio hypothesis because we do not know the adult sex ratio of this population.

Do female cardinals threaten their mates with divorce if male provisioning rates are low? This is not yet known, although we have documented divorces. Data across three years have revealed that, of 10 pairs in which both birds were banded and detected in the following year, two pairs (20%) divorced and eight remained together. In addition, of 21 banded pairs monitored during a breeding season, two (10%) divorced and 19 remained together for all nesting attempts. Based on the findings reported here, we predict that it will be shown that this population of cardinals displays a male-biased adult sex ratio, as is common in socially monogamous passerines (Lack 1954, Breitwisch 1989). If the adult sex ratio is not male-biased, the skewed sex ratio hypothesis would be refuted (Breitwisch 1989).

The positive correlation in feeding efforts between mates is predicted by the assortative mating hypothesis (Burley 1981, 1983, 1986, Breitwisch 1988). We conclude either that birds of similar quality mate assortatively or that females mated to high quality males can benefit from the resources defended by these males and, thereby, match the efforts of their mates. The latter possibility perhaps simply reduces to the former, if high quality females mate with males able to defend high quality territories. These possibilities warrant further investigation.

These data also allow rejection of the deflection hypothesis (Cott 1964, Baker and Parker 1979). The prediction of the deflection hypothesis that extremely dichromatic male cardinals should either refrain from nest visits or, at least, curtail their activity at the nest is refuted. The 57% overall proportion of male feedings places cardinals toward the upper end of the range of male contributions tabulated by Searcy and Yasukawa (1995, p. 260) for a small sample of passerine species, both mono- and dichromatic. It thus seems unlikely that brilliantly-plumaged male cardinals are significantly endangering nest contents in the course of provisioning nestlings. Perhaps this is because the overall nest predation incidence is high and may be largely independent of any defensive efforts by cardinals (Filliater et al. 1994, Nealen and Breitwisch, in press).

Finally, two other hypotheses are yet to be addressed. The honest advertisement of good parenting hypothesis (Hoelzer 1989, Kirkpatrick 1985) predicts that the exaggeration of the male ornament (here, scarlet plumage) will itself predict the level of paternal care. Thus, the relative

contribution to provisioning by a male should be positively correlated with the degree of ornamentation. Second, the "mixed-strategy" hypothesis (Trivers 1972, Westneat et al. 1990) predicts that males display a reproductive strategy involving both parental investment and mating effort expended on attempts to secure extra-pair copulations; as the latter increases, the former is predicted to decrease. Ritchison et al. (1994) suggested several reasons for the relatively low incidence of extra-pair fertilizations in cardinals: proportionately low fitness gains for males from extra-pair copulations relative to paternal effort, female ability to assess male quality prior to mating in this non-migratory species, and diligent male mate-guarding. We currently have no evidence for a mixed strategy in which males expend significant effort in seeking extra-pair copulations.

In summary, these results demonstrate that even in an extremely dichromatic bird species, males may expend significant parental effort, and birds of similar quality may mate with one another. Whether the degree of male ornamentation is related to paternal effort, and thus predictable by females, is yet to be determined.

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Wilson Bull., 109(1), 1997, pp. 154–157

SHORT COMMUNICATIONS

Long-distance dispersal of Red-cockaded Woodpeckers.—Red-cockaded woodpeckers (*Picoides borealis*) are territorial, non-migratory birds that inhabit pine forests of the southeastern United States (Jackson 1971). They may practice two life history strategies. They may remain on their natal area as helper until a breeding vacancy becomes available at that site or nearby, or disperse in search of a breeding vacancy or unoccupied territory (Walters 1990). By remaining as a helper, a male may inherit a territory upon the death of the breeding male. Helpers are typically the sons of the breeding male and may be from one to several years of age (Hooper et al. 1980). Female Red-cockaded woodpeckers almost exclusively disperse from their natal area, while males employ either strategy (Walters 1990). In this note we define dispersal as the movement of a juvenile or helper from its group of origin to the location where it first breeds (Shields 1987) and fledglings are considered to be juveniles at the time of their dispersal.

Seven long-distance dispersal events by adult and juvenile Red-cockaded woodpeckers have been documented in the literature. These movements can be described as intra-population, or more significantly, inter-population which is important for maintaining gene flow among populations. We define an inter-population dispersal as one occurring between populations that have historically been demographically isolated. Maximum intra-population dispersal distances reported for juvenile females and males in the North Carolina Sandhills were 31.5 and 21.1 km, respectively (Walters 1991). In South Carolina, maximum intra-population movements for juvenile females and males were 23.4 km and 22.1 km, respectively, at the Savannah River Site (SRS) (J. Edwards, unpubl. data) and 19.3 km for a juvenile female at Sand Hills State Forest (SSF) (D.P. Ferral, unpubl. data). Intra-population movements for adults have been recorded as 17.1 km for a male in the North Carolina sandhills (Walters 1991), 30.1 km for a male at the SRS (Jackson 1990), and 41.3 km for males in Texas (Lay and Swepston 1973).

Three inter-population dispersal events have been reported: a 73.6 km movement of a juvenile female from a small population (10 groups) in McCurtain County, Oklahoma (John Skeen, pers. comm.) to an equally small population (12 groups) within the Ouachita National Forest in Arkansas (Montague and Bukenhofer 1994; Warren Montague, pers. comm.); 90 km for an adult female in North Carolina that moved from a single isolated group in the North Carolina Piedmont to a large population (450 groups) in the North Carolina Sandhills (Walters et al. 1988); and 66 km for an adult male in Texas that moved from the Angelina National Forest to the Davy Crocket National Forest (R.N. Conner, pers. Comm.).

Here we report on two juvenile Red-cockaded woodpeckers moving even longer distances between populations. On 6 October 1994, we captured an unfamiliar color-banded female at the SSF, Chesterfield County, South Carolina. The capture site was 6.4 km north of the town of Patrick. This bird originated from the Croatan National Forest (CNF) in North Carolina, where it was banded as a nestling on 25 May 1993. It was last observed on the CNF on 11 June 1993 in its natal cluster (Jeff Walters and Jan Goodson, pers. comm.). The banding site was 8 km west of Newport, Carteret County, North Carolina. The distance between banding and capture locations is 287 km and is the longest dispersal recorded for the species (Fig. 1). It paired with a male in April 1995 and fledged two young in June 1995. It is unknown how long the CNF bird had resided at SSF before being recognized. Red-cockaded Woodpeckers at the capture site had successfully nested and fledged young in 1994; however, the breeding pair was not identified. The SSF is a 18,400 ha multiple-use forest containing 46 groups of Red-cockaded Woodpeckers.

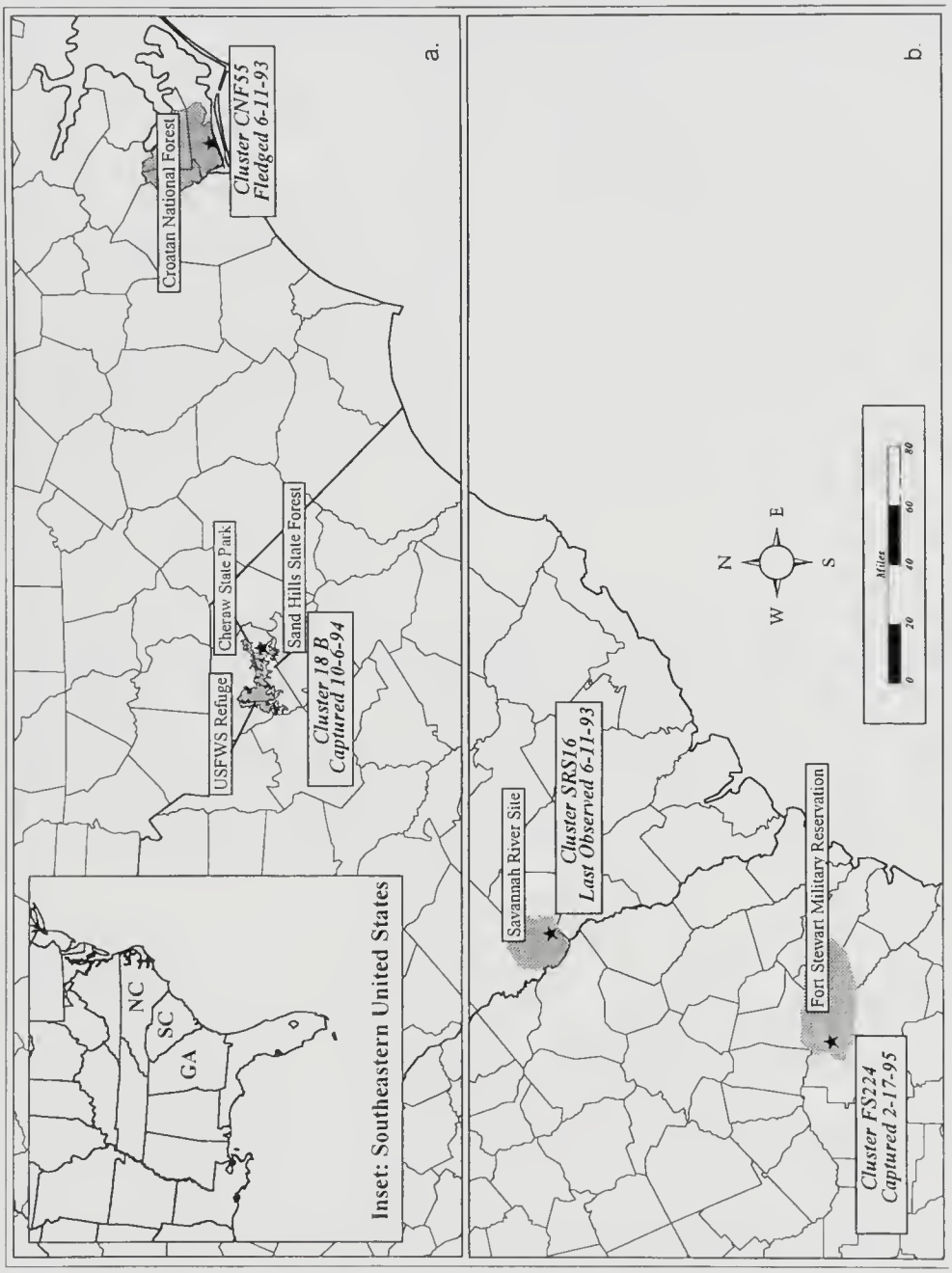

FIG. 1. Two recorded long-distance movements of Red-cockaded Woodpeckers: (a) Two-hundred and eighty-seven km dispersal of a female from the Croatan National Forest, Carteret County, North Carolina to Sand Hills State Forest, Chesterfield County, South Carolina, and (b) One-hundred and sixty km dispersal of a male from the Savannah River Site, Barnwell County, South Carolina, to Fort Stewart Military Reservation, Liberty County, Georgia.

Previous to our report, only one inter-population movement of a male Red-cockaded Woodpeckers had been reported. On 17 February 1995, a male banded as a nestling on the SRS was captured, identified, and released at Fort Stewart Military Reservation, Liberty County, Georgia (Larry Carlisle, pers. comm.). The male fledgling had been banded on 22 May 1992 with a U.S. Fish and Wildlife Service band. It was last observed on the SRS on 11 June 1993 in its natal cluster. It was recovered on 2 February 1995 at Fort Stewart. The distance between banding and capture sites was approximately 160 km (Fig. 1). The bird has not been observed on Fort Stewart since its initial capture.

Dispersal events reported here, and those previously reported, suggest that natural genetic exchanges between geographically isolated populations are more common than previously hypothesized (Walters et al. 1988). Moreover, our ability to document such extreme movements of Red-cockaded woodpeckers results from and demonstrates the utility of long-term banding and monitoring efforts. These findings may also provide new insight into the design and implementation of present and future Red-cockaded Woodpecker translocation programs.

Dispersal between physiographically disparate populations, e.g., from the outer Coastal Plain to the fall line of the Sandhills, demonstrates that dispersers are able to traverse large expanses of unfamiliar habitats. Dispersal events reported by Walters (1990) and Montague and Bukenhofer (1994) are significant in that the birds moved from relatively small to much larger populations, indicating the importance of small, spatially isolated populations. In addition to representing potential genetic variation, these small, isolated populations may also provide temporary stopping points for Red-cockaded Woodpeckers during long-distance movements.

Our findings emphasize that our ability to detect such movements has increased as a result of long-term banding efforts in multiple populations. These interpopulation movements are important in maintaining genetic exchange among Red-cockaded Woodpecker populations.

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D. PAT FERRAL, *Wildlife Diversity Section, South Carolina Dept. of Natural Resources, P.O. Box 167, Columbia, South Carolina 29202*; JOHN W. EDWARDS, *USDA Forest Service, Southern Research Station, Dept. of Forest Resources, Clemson Univ., Clemson, South Carolina 29634* (Present address: *Dept. of Agricultural and Applied Economics, Clemson Univ., Clemson, South Carolina 29634-0355.*); AND AMY E. ARMSTRONG, *Wildlife Diversity Section, South Carolina, Dept. of Natural Resources, P.O. Box 167, Columbia, South Carolina 29202* (Present address: *500 Kinsler Road, Blythewood, South Carolina 29016*). *Received 16 March 1996, accepted 15 Aug. 1996.*

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Long-distance dispersal of Red-cockaded Woodpeckers in Texas.—The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species indigenous to the mature pine forests of the southeastern United States. Continued loss and fragmentation of the mature forests of the South have increased the isolation of extant woodpecker groups throughout the range of this endangered species (USFWS 1985, Conner and Rudolph 1989). Mate replacement following mortality of female and some male breeders is dependent on successful dispersal of young and adult woodpeckers (Walters et al. 1988a). Helper males provide replacements for some male breeders, regardless of cluster isolation.

Dispersal in Red-cockaded Woodpeckers takes two forms, a short-distance form unique to Red-cockaded Woodpeckers, and a longer-distance form like that of other birds (J. R. Walters, pers. commun.). Long-distance dispersal is likely highly sensitive to population density because birds tend to keep moving until they find a breeding vacancy. Isolation of woodpecker groups within a population appears to impair successful short-distance dispersal of woodpeckers and fragmentation of mature pine habitat appears to interfere with successful long-distance dispersal within and between populations to the extent necessary to provide replacement breeders when a member of the breeding pair dies (Conner and Rudolph 1991).

Information on dispersal distances is important in evaluating relationships between cluster isolation and thresholds for successful woodpecker dispersal. Most cases of dispersal involve relatively short distances ($\bar{x}$ = 4.7 km for first-year females, and $\bar{x}$ = 5.4 for first-year males), generally to the closest neighboring woodpecker groups (Walters et al. 1988a). Dispersing adults generally travel shorter distances ($\bar{x}$ = 1.8 km for males and $\bar{x}$ = 2.1 km for females) (Walters et al. 1988a).

Long-distance dispersal that involves movement through nonforest habitat and other possible impediments to dispersal have in the past appeared to be rare, and the paths that Red-cockaded Woodpeckers take through or around such potential barriers are unknown. Walters et al. (1988b) reported a 90 km dispersal by an adult female in North Carolina that included

possible movements through agricultural lands and hardwood forest habitats. Montague and Bukenhofer (1994) reported a 74 km dispersal of a young female Red-cockaded Woodpecker from the McCurtain County Wilderness Area in Oklahoma to the Ouachita National Forest in Arkansas. In November 1995 a female originally banded in Arkansas was recaptured in Louisiana following a 338 km dispersal (Montague et al., pers. commun.). Walters et al. (1988b) and Reed et al. (1988) stressed the importance of dispersal between populations for the maintenance of genetic variability. The extent to which Red-cockaded Woodpeckers disperse long distances becomes increasingly important for both demographic and genetic reasons as the degree of cluster/population isolation and habitat fragmentation increases. In this paper, we describe six cases of long-distance dispersal by Red-cockaded Woodpeckers within and between populations on the Angelina, Davy Crockett, and Sabine National Forests in eastern Texas.

The longest dispersal we observed (75 km straight-line distance) was made by a female Red-cockaded Woodpecker (#1) banded in her natal cluster as a juvenile on 17 October 1989 on the Angelina National Forest (Fig. 1). She was recaptured on 22 September 1993 and again on 13 September 1995 in the Davy Crockett National Forest. If she traveled in a straight line, her dispersal path would have crossed a 5-km wide portion of the Sam Rayburn Reservoir. To avoid the reservoir, her minimal-distance dispersal path would have crossed more than 20 km of agricultural lands, several major highways, and been in excess of 80 km.

Our second longest dispersal (66 km) was made by a male (#2). He was banded as a juvenile in his natal cluster on the Angelina National Forest on 18 September 1990. He was recaptured on 16 October 1991 in the Davy Crockett National Forest (Fig. 1). A straight line dispersal route for this male would have involved crossing a 4 km section of Sam Rayburn Reservoir, > 20 km of agricultural lands, and several major highways. It is interesting to note that this male was the same male that had fallen from its nest cavity as a nestling and was replaced by us on 31 May 1990 (Schaefer et al. 1991). The 66 km dispersal made by this male represents the longest dispersal distance ever reported for a male Red-cockaded Woodpecker. Walters et al. (1988a) observed a maximum dispersal distance of 21.1 km for a fledgling male during their study in the North Carolina Sandhills. Lay and Swepston (1973) reported a 42-km dispersal by a 2+ year-old male Red-cockaded Woodpecker on the Angelina National Forest.

Another male Red-cockaded Woodpecker (#3) made a 49 km dispersal from the Angelina National Forest to the Sabine National Forest. He was banded as a juvenile in his natal cluster on 29 September 1994 and recaptured on the Sabine National Forest on 28 September 1995 (Fig. 1). A straight-line dispersal path would have included > 15 km of agricultural lands.

Three additional cases of long-distance dispersal by females occurred within the Angelina National Forest (Fig. 1). A female (#4) was banded on 19 May 1994 as a nestling on the Sam Houston National Forest. She was recaptured as a juvenile on 12 December 1994 and translocated to the Angelina National Forest on 13 December 1994 where she was released into a cluster containing a single male. On 24 August 1995 female #4 was recaptured on the Angelina National Forest after dispersing a least 30 km (straight-line distance). This 30 km distance included a 7 km span of Sam Rayburn Reservoir. To avoid crossing this large reservoir, she would have had to travel > 80 km (Fig. 1). Another female Red-cockaded Woodpecker (#5) was banded as a juvenile in her natal cluster on 10 September 1991 on the Angelina National Forest. She was recaptured on 26 August 1995 in another area of the Angelina National Forest 28 km from her natal cluster. To avoid an 8 km span of the Sam Rayburn Reservoir she would have had to fly > 80 km (Fig. 1). Another female (#6) was banded as a juvenile in her natal cluster on 6 December 1989 on the Angelina National Forest and was recaptured on 29 August 1994 in a different forest compartment. A straight-

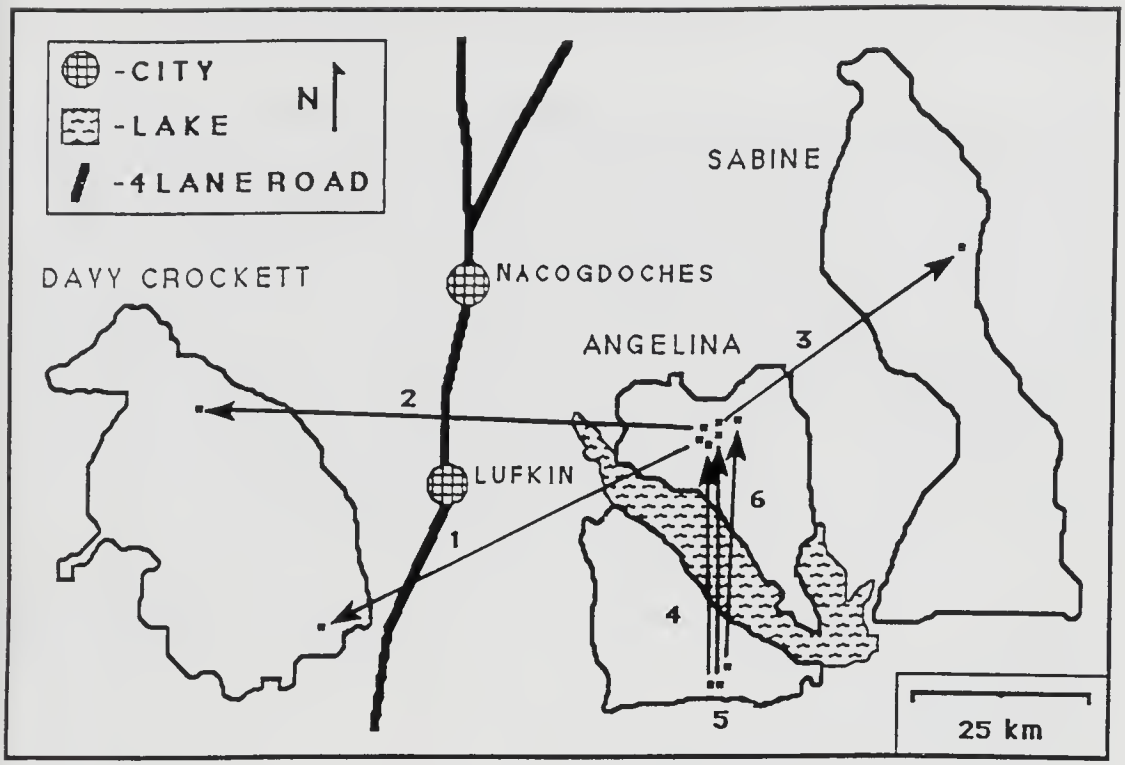

FIG. 1. Six instances of long-distance dispersal by Red-cockaded Woodpeckers on the Angelina, Davy Crockett, and Sabine National Forests in eastern Texas from 1989 to 1995. The dispersal lines represent the straight-line distances between clusters where woodpeckers were initially captured and sites of subsequent recapture. Numbers associated with dispersal lines on the map correspond to Red-cockaded Woodpecker numbers in the text.

line dispersal of 36 km would have included a 9 km span of the Sam Rayburn Reservoir. Otherwise, a dispersal of > 85 km would have been required to avoid crossing the reservoir (Fig. 1).

Although the cases of dispersal we observed are not as long as the 90 km distance reported by Walters et al. (1988b), they suggest that long-distance dispersal may occur on a fairly regular basis. Our observations also indicate that Red-cockaded Woodpeckers have the ability to cross or circumnavigate large, non-forest landscape features such as agricultural lands and reservoirs. This is particularly important for the maintenance of genetic diversity in small, satellite populations of woodpeckers (Haig et al. 1993). We do not know if the long-distance dispersal results in a higher mortality rate to dispersing individuals.

The intensive six-year demographic study by Walters et al. (1988a) in North Carolina involved monitoring a population of over 500 banded Red-cockaded Woodpeckers, and initially, only one individual (a female) was detected dispersing over 30 km (31.5 km) prior to the 90 km dispersal reported later (Walters et al. 1988b). The six cases of long-distance dispersal we observed were detected from 122 banded woodpeckers over a similar six-year period. Obviously, the observations we report here do not represent all instances of long-distance dispersal by Red-cockaded Woodpeckers on the National Forests in Texas, but are only those detected under a limited banding and recapture program. Most woodpeckers were banded to assist with the U.S. Forest Service's translocation program to augment clusters that contained only a single woodpecker, and not as a major demography study such as that of Walters et al. (1988a). Thus, what we have observed likely under represents long-distance

dispersal by Red-cockaded Woodpeckers among the small, isolated populations in eastern Texas.

The apparent higher frequency of long-distance dispersal we detected among the small, isolated populations in eastern Texas suggests the possibility that long-distance dispersal may be more prevalent within small populations where population density is low than within larger, dense populations such as those reported in the North Carolina Sandhills (Walters et al. 1988a). Thus, small, isolated populations may not be as genetically isolated as previously thought and loss of genetic variability may not be as great as has been assumed when defining minimum viable population size based on genetic criteria. However, long-distance dispersal by woodpeckers into large, dense populations appears to have a higher probability than long-distance dispersal into small, isolated populations because of the different sizes of the respective "target" populations.

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Factors affecting the survival of Ovenbirds wintering in the Northeast.—The northern limit of the usual winter range of the Ovenbird (*Seiurus aurocapillus*) is coastal North Carolina (ca 36°N latitude; Root 1988a), with casual winter occurrences as far north as the Great Lakes region and New England (AOU. 1983). In general, the Ovenbird does not winter in areas where the average minimum January temperature is less than about 0°C and it is most abundant where this temperature is about 10°C (i.e., southern Florida; Root 1988a). Among the wood warblers, only the Yellow-rumped Warbler (*Dendroica coronata*) routinely winters where average minimum January temperatures are below freezing (Root 1988a). This is probably because the generalized foraging behavior (Morse 1989) and specialized gastrointestinal traits of the Yellow-rumped Warbler (Place and Stiles 1992) enable it to exploit alternative, energy-rich food resources, such as bayberry (*Myrica* spp.) available in these areas (Wilz and Giampa 1978).

In addition to labile feeding habits and specialized digestive physiology, other behavioral and physiological adaptations, such as huddling, roosting in protected sites, facultative migration, and nocturnal hypothermy may enhance the ability of largely insectivorous birds to survive winter in cold climates (Frazier and Nolan 1959, Kendeigh et al. 1977, Blem and Pagels 1984, Walsberg 1985, Terrill and Ohmart 1984). Without such adaptations, species such as the Ovenbird are not expected to survive the winter at more northerly latitudes due to energetic constraints (Seibert 1949; Root 1988b, 1989). Observations of birds attempting to winter beyond the normal range of their species can provide empirical evidence to test this prediction and may help clarify environmental and other factors that influence winter distributions.

Study area and methods.—On 4 Jan. 1983 an Ovenbird appeared outside the bird banding laboratory at Powdermill Nature Reserve, Carnegie Museum of Natural History's field research station, three miles south of Rector, Westmoreland County, Pennsylvania (40°10′N, 79°16′W). In the mountain valley in which Powdermill is situated, minimum January temperatures average < -5°C and regularly drop below -17°C (J. F. Merritt, unpubl. data). This sighting provided just the second winter occurrence of the species in western Pennsylvania and the first January record; subsequently, an Ovenbird was seen at Warren in northwestern Pennsylvania as late as 27 Jan. 1988 (Hall 1988). The species has never been observed in western Pennsylvania in February or March (Leberman 1988), suggesting that it may be incapable of maintaining a positive energy balance for the duration of the winter at this latitude. What makes the Powdermill record noteworthy is that the bird was captured, banded, and rehandled twice in the space of two weeks (body mass and subcutaneous fat levels were recorded each time), in addition to being observed almost daily during the same period.

We used our observations of foraging behavior and body mass variation in this bird, correlated to local weather data, to assess possible factors affecting the survival of individuals that attempt to winter north of the usual winter range of this species. Because little can be confidently concluded from our data for a single Ovenbird, we also reviewed extralimital winter records of the species (i.e., birds seen between December and March at sites north of 38°N latitude) published in *Audubon Field Notes* and *American Birds* from 1970–1995.

Results and discussion.—We captured the Ovenbird at 11:45 h (EST) on 8 Jan. in a mist net erected near a thicket and bird feeding area adjacent to our banding lab. We identified it as a bird hatched in the previous calendar year ("SY" in banding terminology), based on retained juvenal wing feathers (see Mulvihill 1993); its skull was completely pneumatized. Its unflattened wing chord measured 74.0 mm, and we judged it to have moderate subcutaneous, furcular fat deposits, rating a "2" on a scale of 0–3 (none to fat mounded; Leber-

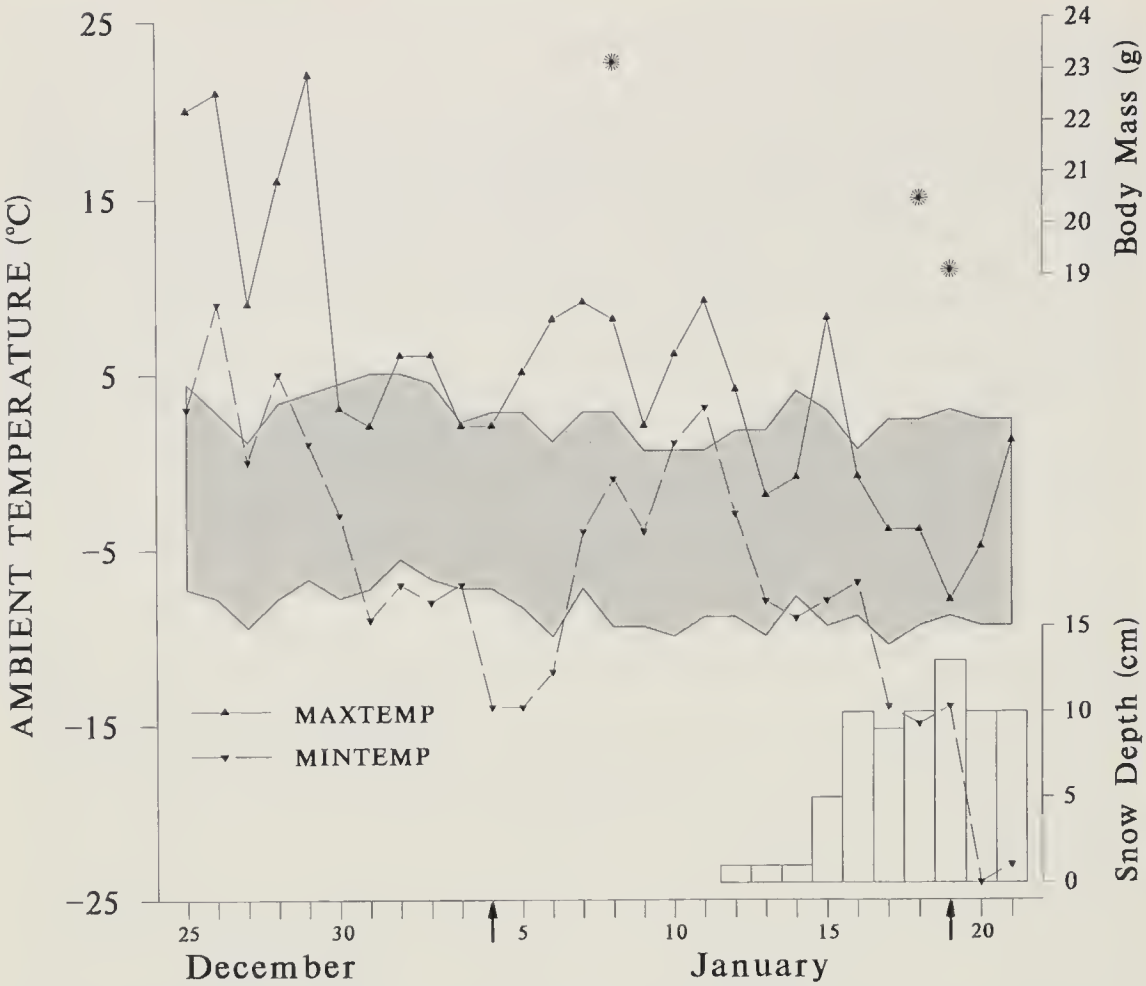

FIG. 1. Ambient temperatures and snow cover in relation to body mass measurements of an Ovenbird banded and recaptured at Powdermill Nature Reserve in southwestern Pennsylvania. The shaded area shows average daily minimum and maximum temperatures recorded at Powdermill Nature Reserve from 1972–1995. First and last seen dates for the bird are shown by arrows on the *x*-axis.

man 1967). It weighed 23.2 g and appeared healthy with no aberrations or indications of earlier injury. Its body mass at first handling exceeded all mean monthly values for the species at Powdermill from April–October (Clench and Leberman 1978). Local weather prior to the Ovenbird's capture was unseasonably mild, with daytime temperatures well above freezing and no snowcover (Fig. 1). Nonetheless, the Ovenbird had survived several nights with below freezing temperatures, apparently in good condition. It may have been the very cold overnight minimum temperature on 3–4 Jan. (Fig. 1), however, that caused the Ovenbird to seek out the bird feeding area beside our banding lab in the first place.

During the period of comparatively mild weather from 5–12 Jan., when daytime high temperatures were well above freezing and there was no snowcover (Fig. 1), the Ovenbird often fed on the lawn immediately adjacent to the banding lab, usually within a few feet of our windows. The Ovenbird's foraging behavior suggested that it was searching for and finding small invertebrate prey; on several occasions we observed it feeding on earthworms. Sprunt (1957) reported the Ovenbirds' food habits as "Largely insectivorous but also ground life, such as snails, slugs and earthworms. A few seeds and fruits taken at times."

After 12 Jan., the weather worsened with colder temperatures and light snowcover (Fig. 1). During this time we kept some grassy areas free of snow and turned sod in a few places to expose buried invertebrate prey. We observed the Ovenbird using these areas, as well as a narrow strip of grass sheltered from the snow by an overhanging roof. Following heavier snowfalls on 15–16 Jan., it was no longer able to forage for invertebrates and joined many other birds feeding at scattered seed piles on top of the snow. The Ovenbird ate mostly white millet and interacted with several species at the seed piles, especially Dark-eyed Juncos (*Junco hyemalis*), White-throated Sparrows (*Zonotrichia albicollis*), Song Sparrows (*Melospiza melodia*), American Tree Sparrow (*Spizella arborea*), and Tufted Titmice (*Parus bicolor*). It was rarely displaced by any of these birds and was seen to initiate and win aggressive encounters with several of them, at times monopolizing a seed pile for several minutes.

At 10:45 h (EST) on 18 Jan., we recaptured the Ovenbird in a four-cell, Potter-type wire trap placed on the ground and baited with seed. Compared to its initial capture, the Ovenbird had lost 2.7 g and had no visible fat deposits. We recaptured it a second time, again in a wire ground trap, at 11:40 h (EST) on 19 Jan. At this handling it had lost an additional 1.4 g and again had no visible fat deposits. Following its release, the Ovenbird resumed feeding on bird seed. Overnight temperatures (early morning 20 Jan.) dropped to −24°C (Fig. 1), and we did not see the bird the following day. Temperatures the next night fell to −23°C, and although the daytime high temperature on 21 Jan. was above freezing, we did not observe the Ovenbird.

Since it had been seen daily for over two weeks, we assume that the Ovenbird starved during the long, bitterly cold night of 19–20 Jan. Its last recorded body mass, 19.1 g on 19 Jan., was similar to lean body mass values of Ovenbirds caught in Jamaica from October to February (Diamond et al. 1977) and to the average body mass of the species from June through August at Powdermill (Clench and Leberman 1978). The similarity of the Ovenbird's mass to that of breeding birds at Powdermill suggests that it had depleted most, if not all, of its usable lipid reserves (Blem 1990). The observed mass loss, 18% overall 7% between the last two handlings, showed that it was not maintaining a positive energy balance immediately prior to the night of 19–20 Jan.

Root (1988c) observed that the northern winter distribution limits of many species coincide with average minimum January temperature isotherms, and later sought a physiological basis for this observation (Root 1988b). She concluded, based on estimates of the resting metabolic rate of several of these species at the northern edge of their winter range, that passerines showing this distributional pattern are restricted to areas where they do not need to raise their "northern boundary metabolic rate" (NBMR) more than 2.45 times their basal metabolic rate (BMR) in order to counteract the effects of low ambient temperature. She suggested that the consistency of this relationship across many species " demonstrates a physiological limit imposed by ambient temperature regardless of body size, diet, or general habitat" (but see Castro 1989).

Using Root's (1988b) equations (2), (8), and (9), we estimated the 19 g Ovenbird's BMR as 24.2 $kJ \cdot d^{-1}$, thermal conductance (COND) as 1.45 $kJ \cdot (d \cdot bird \cdot °C)^{-1}$, and lower critical temperature (TCRIT) as 24°C. Using these values, and the average minimum January temperature (0°C) at the species' northern distribution limit (TDIST), we estimated its NBMR, according to Castro's (1989) corrected form of Root's (1988b) Eq. 1:

$$NBMR = COND \times (TCRIT - TDIST) + BMR \quad (1)$$

We calculated the Ovenbird's NBMR as 59.0 $kJ \cdot d^{-1}$ or 2.44 times BMR, in close agreement with Root's (1988b) proposed "physiological limit" of 2.45 times BMR; substituting the

average minimum January temperature at Powdermill (−5°C) for TDIST raised NBMR to 2.8 times BMR.

Using the same equation, we estimated the Ovenbird's metabolic rate during the 24-h period between its last two captures (average temperature −10°C) as 73.5 $kJ \cdot d^{-1}$, which would give a mass loss of 1.9 g if the bird were metabolizing fat (caloric density of fat = 37.7 $kJ \cdot g^{-1}$). The bird actually lost 1.4 g during the period, suggesting that it had some remaining fat reserves (probably intraperitoneal fat, since it had no visible subcutaneous fat at the beginning of the period) and may even have gained some metabolizable mass while feeding during the daylight hours of 18 Jan. It clearly was experiencing a negative energy balance at this time, however, and by the end of the day on 19 Jan. likely had depleted all of its fat reserves.

Finally, we estimated the Ovenbird's metabolic rate on the night of 19–20 Jan. (assuming an average overnight temperature of −16°C) would have been 82.2 $kJ \cdot d^{-1}$ or 3.4 times BMR. In the absence of any energy-conserving physiological or behavioral adjustments, a minimum fat deposit of 1.3 g would have been needed to fuel the Ovenbird's metabolism for an inactive period of 14 h on the night of 19–20 Jan. (overnight metabolic demand = 48 kJ; caloric density of fat = 37.7 $kJ \cdot g^{-1}$). The body mass of the Ovenbird reported on here varied by 2.7–4.1 g between a lean (fat score "0") and moderately fattened (fat score "2") condition. On average, Ovenbirds add 1.5 g to their body mass for each increase in fat score, giving an average gain 4.5 g between a visibly lean and a maximally fattened condition (Mulvihilll, unpubl. data). Although these data suggest that the Ovenbird was physiologically capable of accumulating more than enough fat to meet increased metabolic demands associated with extremely cold temperatures, it clearly was unable to locate food resources of sufficient quantity or quality to do so immediately prior to the night of 19–20 Jan.

We cannot pinpoint when the Ovenbird first began to deplete its fat reserves, but we think that this probably occurred after deep snowcover made it impossible for this ground-foraging species to find invertebrate prey. Extending the Ovenbird's rate of mass loss for the 24-h period from 18–19 Jan. (0.11 $g \cdot h^{-1}$) backward to 16 Jan., the day when deep snowcover forced it to feed exclusively on bird seed, we reach a body mass similar to that recorded during the bird's initial handling on 8 Jan. (Fig. 1). The largely insectivorous Ovenbird presumably lacks of the morphological and physiological specializations that enable granivorous birds to digest seeds efficiently (Ziswiler and Farner 1972), and reduced metabolizable energy intake on a seed diet (Kendeigh et al. 1977) would explain its inability to maintain fat reserves after 15 Jan. The possibility that the Ovenbird may have maintained a favorable energy balance for more than a week before and after its initial capture, despite minimum temperatures that were mostly well below freezing during this time, suggests that the species could successfully winter in areas that are colder on average, were it not for the likelihood of deep and persistent snowcover in these same areas.

In our review of the literature, we found a total of 80 extralimital winter records of the Ovenbird, including at least one record in each of the 25 seasons that we surveyed. The distribution of these records by month (last seen dates) was December, 61%; January, 25%; February, 9%; March, 5%. In general, multiple records of Ovenbirds (up to eight in 1983–1984; seven in 1990–1991) occurred during winters or portions of winter seasons that were characterized as unusually mild with little or no snowcover. In several cases where an Ovenbird was observed daily at a site for a week or more, the date when it was either last seen or found dead corresponded closely with the onset of a period characterized by *both* cold temperatures and significant snow accumulation. In two cases, Ovenbirds disappeared following severe winter storms that were described as "blizzards;" one of these Ovenbirds, however, apparently had earlier survived a prolonged period of very cold temperatures and

deep snowcover by feeding on table scraps and hamburger at a feeder in Plainfield, New Jersey (Paxton et al. 1978). Of four Ovenbirds believed to have survived the winter at northerly latitudes, individuals at feeders in eastern Pennsylvania from 15 Jan.–4 Mar. 1975 (eating suet and peanut butter; M. and J. Dye, pers. comm.) and southeastern New York from 7 Jan.–3 Mar. 1979 (eating mostly small seeds; Richards et al. 1980), as well as a bird observed in northeastern New York on 30 Mar. 1975 (Buckley and Kane 1975), all experienced winters that were unusually mild and pratically devoid of snow cover (Buckley and Kane 1975, Scott and Cutler 1975, Richards et al. 1980). One Ovenbird, however, apparently survived away from feeders at Brunswick, Maine, during the winter of 1983–1984, where the weather was described as mild in December and February but frigid and snowy during most of January (Heil 1984).

In general, the Ovenbird's northern winter range boundary and associated NBMR fit Root's (1988b) model of a generalized energy constraint on the distributions of many bird species. Notwithstanding this, our data on body mass and fat reserves for an extralimital Ovenbird, along with published records documenting the overwinter survival of Ovenbirds at northerly latitudes, demonstrate that this species is capable of meeting energetic demands associated with average mid-winter temperatures that would theoretically require it to raise its metabolic rate much more than 2.45 times its BMR. The factors that limit an Ovenbird's survival at northern latitudes apparently are those affecting its ability to accumulate and maintain energy reserves sufficient to accomodate simultaneously sharply increased metabolic demand and decreased metabolic energy intake associated with extreme climatic conditions (see Blem 1990). The likelihood that complex, species-specific interactions among several environmental, behavioral, morphological, and physiological variables underlie the simple isothermal associations of avian distribution limits (Root 1988b, cf. Seibert 1949) should serve as a caution in interpreting the among-species patterns produced by those associations (see also King 1974).

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ROBERT S. MULVIHILL AND ROBERT C. LEBERMAN, *Section of Birds, Carnegie Mus. Nat. Hist., Powdermill Nat. Res., HC 64, Box 453, Rector, Pennsylvania 15677-9605.* *Received 22 Feb. 1996, accepted 25 April 1996.*

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Nesting of Lesser Nighthawks on beaches in El Salvador.—Distribution of the Lesser Nighthawk (*Chordeiles acutipennis*) in northern Central America is poorly understood (Howell and Webb 1995). We here present the first documentation of breeding for the species in El Salvador, as well as the first documentation of breeding in association with terns and plovers.

On 4 June 1994 we found six Lesser Nighthawk nests near the mouth of the Río Lempa, in the Dept. of San Vicente, El Salvador (13°15′N, 88°49′W). Lesser Nighthawks deposit their eggs on the bare ground (Bent 1940:246), here referred to as a "nest." The nighthawks appeared to have formed a breeding colony at the site, since extensive similar habitat nearby was devoid of the birds. We estimate that this colony contained between eight and 15 breeding pairs, based on the numbers of adults (24–30) and fledged juveniles (3) present. The minimum estimate assumes that the colony contained the six observed nests plus two other nests from which the observed juveniles fledged, since Lesser Nighthawks lay only two eggs per nest. The upper estimate is half of the high estimate for number of adults present. Three of the nests contained one egg, two nests contained two eggs, and one contained a hatchling. The eggs were laid directly on the hot sand and were behind the high tide line where sparse beach grass or other beach vegetation grew. About 25 m separated the two closest nests. We measured six eggs; all were 20 × 28 mm (range for length 26 to 30).

Beach-nesting colonies of Lesser Nighthawks have been reported only anecdotally from Costa Rica (Stiles and Skutch 1989); the formation of colonies by this species has not been reported outside of Costa Rica. Our observations represent the first documentation of the behavior from northern Central America.

One of us (WR) found a second nesting site on 13 June 1994, apparently just one nest (only one adult was observed), on the open sand behind the high tide line, at Arcos del Espino, a beach in the Dept. of Usulután, El Salvador (13°11′N, 88°21′W). The nest contained one egg. The nest was within 15 m of a small colony (four nests) of Least Terns (*Sterna antillarum*). Two observations indicate that breeding occurs at other beach sites with similar habitat. On 30 July 1994, we found 11 nighthawks at a tiny island in the Bahía de Jiquilisco and suspect that breeding may occur on the nearby San Juan del Gozo peninsula, Dept. of Usulután. At Punta La Chepona on Isla San Sebastián, Dept. of Usulután, we observed one juvenile and four adult Lesser Nighthawks on 31 July 1994.

We estimate that nighthawks nest in El Salvador at least from 25 April through 5 July, although these dates could vary by two weeks or so (11 April through 20 July). Our prediction is based on an incubation period of 18–19 days and fledgling period of three weeks as reported by Pickwell and Smith (1938) for the northern subspecies Texas Nighthawk (*C. a. texensis*). The breeding season may in fact begin in March, as reported by Stiles and Skutch (1989) for Costa Rica. The Texas Nighthawk found in the southwest U.S. regularly incubates eggs late April through early July (Bent 1940:253), and the latest reported incubation date is 6 August in Arizona (Bendire 1895).

Howell and Webb (1995:373) suggest that resident Lesser Nighthawks in northern Central America breed mainly in the dry interior valleys, based on the existence of June specimens and their personal observations of singing nighthawks in late May 1988 in Depto. El Progreso, Guatemala, and at Santa Barbara, Honduras (Steve N. G. Howell, pers. comm.). However, we can not find any documentation of breeding for that region. The A.O.U. checklist (American Ornithologists' Union 1983:308) gives the breeding distribution in Middle America as lowlands of Mexico, Guatemala, and Belize; in Honduras, in the arid interior valleys of the Caribbean drainage; in Nicaragua, at Tipitapa; and in Costa Rica, in Guanacaste province and near Puerto Cortés. The information in the A.O.U. checklist appears to come from unpublished sources or is presumed from the existence of breeding season rec-

ords (without evidence of nesting). For example, in Honduras Monroe (1968:162) reports that there is "no direct evidence" of breeding but specimens were collected in June. In Guatemala, Land (1970:144) reports the species as a probable resident with "no definite nesting records." Dickerman (1985) collected Lesser Nighthawks on the Pacific coast of Guatemala but did not report evidence of breeding. The Nicaragua record, however, is based on a fledgling and adult female collected 28 April 1917 by Miller and Griscom (Thomas Howell, pers. comm.).

On several occasions, we observed Lesser Nighthawks performing distraction displays. Some adults flew slowly near us, calling loudly (a frog-like trill), as if to solicit our attention. Females that we flushed from nests often appeared to fly with difficulty, landing not far away. Twice they landed on the ground nearby with one wing extended, feigning injury. These birds later flew away with no difficulty. Similar distress-simulation and distraction behavior was carefully described for *C. a. texensis* by Pickwell and Smith (1938). We did not observe any aggressive behavior toward us by the nighthawks.

In El Salvador, the Río Lempa colony of Lesser Nighthawks was adjacent to a loose colony of Wilson's Plovers (*Charadrius wilsonia*), which may have provided some protection to the nighthawks by their warning of intruders. At Arcos del Espino, Least Terns aggressively defending their nests would have inadvertantly defended the nighthawk's nest as well. In Peru, Groom (1992) found that Sand-colored Nighthawks (*Chordeiles rupestris*) nesting within 30 m of tern nests benefited directly from terns' aggressive attacks on predators.

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Oliver Komar, *Dept. of Zoology, Ohio Wesleyan Univ., Delaware, Ohio 43015*, and Wilfredo Rodríguez, *Escuela de Biología, Univ. de El Salvador, Ciudad Universitaria, San Salvador, El Salvador.* *Received 4 April 1996, accepted 10 Sept. 1996.*

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Possible use of wading birds as beaters by Snail Kites, Boat-tailed Grackles, and Limpkins.—Foraging in single- or mixed-species flocks is common among many bird species, and the advantages of being in these flocks have been the focus of several investigations (reviewed by Moynihan 1962, Bertram 1978). It has been hypothesized that birds occurring in mixed-species flocks gain advantages from (1) reduced predation risk (e.g., Moynihan 1962, Morse 1970), (2) increased foraging efficiency (e.g., Moynihan 1962, Morse 1970), or (3) social learning (e.g., Ward and Zahavi 1973). Here, we report the anomalous occurrence of flocks consisting of species not typically found in the types of aggregations we describe and suggest the possible function of these aggregations with respect to these hypotheses.

Wading birds commonly forage in mixed-species flocks in the tropics (Caldwell 1981), and both White Ibis (*Eudocimus albus*) and Great Egrets (*Casmerodius albus*) are well known to forage in large groups in the Everglades (Kushlan and Bildstein 1992, Bancroft and Sawicki 1995). In contrast, Snail Kites (*Rostrhamus sociabilis*) may roost and nest communally with or without other species (reviewed by Sykes et al. 1995) but are not reported to forage in mixed-species flocks, even though birds often do forage in proximity to conspecifics. Boat-tailed Grackles (*Quiscalus major*) commonly forage in small single-species groups (e.g., 2 or 3) and occasionally forage in mixed-species flocks with other icterid species (G. T. Bancroft, pers. comm.). They will occasionally attempt to pirate apple snails (*Pomacea paludosa*) from Limpkins (*Aramus guarauna*) or Snail Kites (Snyder and Snyder 1969). However, they are not generally known to forage in large mixed-species flocks with wading birds or Snail Kites (G. T. Bancroft, pers. comm.). Limpkins also are not reported to forage, nest, or roost in large groups (D. Bryan, pers. comm.).

Study area and methods.—We intermittently observed foraging flocks of White Ibis, Great Egrets, Boat-tailed Grackles, Snail Kites, and single-species flocks of Limpkins between 30 December 1993 and 30 January 1994 on and adjacent to the Miccosukee Indian Reservation in Water Conservation Area 3A, Broward County, Florida. The study area consisted primarily of wet prairie habitats comprised mostly of spike rush (*Eleocharis* sp.), maidencane (*Panicum* sp.), and sawgrass (*Cladium jamaicense*) interspersed with linear strands of cypress (*Taxodium ascendens*). Water depths in the wet prairie communities at the time of this study were approximately 10–20 cm.

Our observations consisted of locating individual radio-transmittered Snail Kites as part of a larger ongoing study of survival and movements of Snail Kites throughout Florida. For each transmittered bird, we recorded whether or not they were associated with a flock. We defined a flock as a group of individuals in close proximity (i.e., most individuals were < 10 m from their nearest neighbor) and moving in concert (Hutto 1987). The flocks described here were clearly not merely chance aggregations, but rather were maintaining the association by shifting foraging locations in concert. When the wading birds moved, the Snail Kites and Boat-tailed Grackles followed them within a few minutes. Similarly, when part of a Limpkin flock flew to a new location the remainder of the flock followed over a period of several minutes such that they all appeared to end up at the new location.

In addition to radio-transmittered bird locations, we also conducted a count in which we systematically traversed the wet prairies north to south (using a Global Positioning System and the linear strands of cypress to avoid overlap of areas) and recorded the number of individuals of each species for all flocks we observed. This count was conducted on one day (17 January 1994) to avoid the potential for recording the same flock on several occasions. We also used the presence of known individual radio-transmittered kites to maintain the independence of our observations by assuring that each observed flock had been counted

only once. To prevent double counting, we checked each flock encountered for the presence of radio-transmittered kites and did not count any flock in which a previously encountered radio-transmittered bird was present in case the flock had moved (N = 1 flock).

White Ibis were the most difficult species to count because foraging birds were well concealed in the grass and movements usually were in large groups. Consequently, we had to flush the ibis after counting the kites and grackles in order to estimate flock size. We then made a crude estimate of flock size by actually counting small numbers (e.g., 25) and estimating how many of that group size were within the whole flock. Limpkins also had to be counted after being flushed. However, unlike White Ibises, Limpkins did not flush synchronously but rather flushed in small groups (e.g., 5–20) over a period of several minutes. Consequently, we were able to count the number of Limpkins directly. Great Egrets also occurred in large flocks but were somewhat easier to count than White Ibis or Limpkins because their larger size and erect foraging profile enabled visual observation without having to flush the birds. Boat-tailed Grackles and Snail Kites were relatively easy to count because they perched on small trees adjacent to the foraging ibis. Logistical constraints precluded counting individual or small groups of Boat-tailed Grackles that were not associated with mixed-species flocks. Thus, our summary statistics for this species apply only to birds associated with mixed-species flocks.

We used Pearson's product moment correlation (SAS Inc. 1988) to examine the relationships among group sizes of individual species. Prior to this procedure, we tested for normality of the data for Snail Kites, Boat-tailed Grackles, and combined wading birds (i.e., White Ibis and/or Great Egrets) using a Shipiro-Wilks statistic (SAS inc. 1988) and failed to reject the assumption of normality (at $\alpha = 0.05$) for any of these data. We did not include Little Blue Herons or Tricolored Herons as part of the wading-bird flock size because these species, although sometimes present, often foraged adjacent to the primary flock.

Results.—We observed two primary types of flocks: (1) mixed-species flocks consisting of White Ibises or Great Egrets, in association with Boat-tailed Grackles and Snail Kites, and (2) single-species flocks of Limpkins (Table 1). Although we observed some grackles in proximity to flocks of Limpkins, we did not consider these mixed-species flocks because it was not apparent that the grackles moved in concert with the Limpkins. These were more likely opportunistic aggregations. We did not observe any flocks of White Ibises or Great Egrets during this period without kites and grackles present. Similarly, all radio-transmittered Snail Kites (N = 56 locations of 14 Snail Kites) in this vicinity and located during this period were associated with mixed-species flocks. We did, however, observe several grackles in the area which were not associated with mixed-species flocks. Limpkins were not associated with the other species, except that a few grackles (usually <10) may have been in proximity to Limpkin flocks.

Not all species appeared to maintain actively the mixed-species associations. Rather, White Ibises and Great Egrets appeared to move independently of the kites or grackles and were subsequently followed within a short period of time (usually < 5 min). Wading bird species acted as "core" species of mixed-species flocks with other species as "followers" has previously been reported (e.g., Kushlan 1978, Caldwell 1981).

Our estimates of White Ibis flock size ranged from 50–450 individuals per flock ($\bar{x}$ = 205, SD = 160, N = 6). The flock size of Great Egrets ranged from 90–150 ($\bar{x}$ = 120, SD = 42, N = 2). Numbers of Snail Kites per flock ranged from 4 to 54 ($\bar{x}$ = 21, SD = 18, N = 8). Numbers of grackles per flock ranged from 8–79 ($\bar{x}$ = 31, SD = 23, N = 8). Numbers of Limpkins (not all were in flocks) ranged from 1–116 ($\bar{x}$ = 22, SD = 34, N = 12).

There was a significant correlation between the number of Snail Kites and the number of wading birds (White Ibises and/or Great Egrets)(r = 0.79, P = 0.02). There were weaker

TABLE 1

NUMBER OF SNAIL KITES, BOAT-TAILED GRACKLES, WHITE IBISES, GREAT EGRETS, LIMPKINS, AND OTHER SPECIES COUNTED IN EACH FLOCK OR SOLITARY BIRD ENCOUNTERED ON 17 JANUARY 1994

Snail Kites	Boat-tailed Grackles	White Ibises	Great Egrets	Limpkins	Other[a]
6	27	0	90	0	15
4	8	0	150	0	7
12	19	50	0	0	0
54	79	450	0	0	0
19	43	75	0	0	0
28	31	350	2	0	2
37	11	175	0	0	0
8	28	130	0	0	0
0	0	0	0	2	0
0	0	0	0	23	0
0	0	0	0	17	0
0	7	0	0	116	0
0	3	0	0	57	0
0	0	0	0	1	0
0	0	0	0	2	0
0	0	0	0	7	0
0	4	0	0	34	0
0	0	0	0	1	0
0	0	0	0	2	0
0	0	0	0	3	0

[a] Little Blue Herons and Tricolored Herons.

correlations between numbers of Boat-tailed Grackles and wading birds ($r = 0.64$, $P = 0.08$) and between Snail Kites and Boat-tailed Grackles ($r = 0.66$, $P = 0.07$).

Discussion.—Reduced predation risk was unlikely to have caused the formation of these flocks because the risk of predation for adult herons and Snail Kites is relatively low (Caldwell 1981, Sykes et al. 1995). In addition, the primary predator of adult Snail Kites is probably the Great-horned Owl (*Bubo virginianus*)(Sykes et al. 1995), which would not have been a major threat during diurnal feeding. Social learning is also unlikely to have caused the formation of these flocks because herons frequently return to the same general area for feeding, making the need for social information unnecessary (Caldwell 1981). Additionally, the primary prey of the kites, grackles, and Limpkins during this period was apple snails, whereas adult apple snails would have been unlikely to have been anything more than an occasional food item for the "core" wading bird species (P. Frederick, pers. comm.). Consequently, there would have been little advantage for birds feeding on apple snails to gain information on the foraging location of birds feeding on other prey. Our observations were, however, consistent with the hypothesis of increased foraging efficiency (although not through social learning).

Based on hundreds of hours of field observations of Snail Kites in Florida, it was apparent that food intake by these birds in mixed-species flocks was extremely high. Unfortunately, these flocks persisted for only 4–5 weeks and had dissipated before we had an opportunity

to measure food intake rates directly. However, casual observations of foraging birds (≈ 12–16 h over the study period) indicated that Snail Kites often took less than one minute of flight time to capture a snail, considerably shorter than times previously reported (e.g., reviewed by Sykes et al. 1995). We have no such experience with which to compare Boat-tailed Grackles or Limpkins; however, both appeared to be capturing apple snails with little difficulty.

One strategy of mixed-species group foraging that has been previously reported, particularly in association with Ciconiiformes, is the use of beaters (e.g., Courser and Dinsmore 1975, Kushlan 1978, Russell 1978). In this strategy, individuals of a group flush prey as a result of their activity, which then enhances the opportunities for other individuals (Rand 1954). Snail Kites and Boat-tailed Grackles were mostly foraging among the wading birds rather than merely in their vicinity. They also actively followed the foraging flocks of wading birds. This suggests some advantage associated with the wading birds themselves, rather than just mutual attraction to areas of high prey density. We suggest that the kites and grackles were using the wading birds as beaters. During this time we observed that the physical disturbance from our air boat in the water sometimes revealed live floating apple snails. We checked several snails to confirm that they were alive and their visible presence would usually be short lived, as they dropped in the water column very shortly after the disturbance. We believe that the shallow water in combination with disturbance of the substrate from the foraging wading bird flocks provided a short burst of availability of apple snails, which was the primary prey for the three species (Snail Kites, Boat-tailed Grackles, and Limpkins) not typically found in foraging flocks.

This potential explanation still leaves unanswered why Limpkins were in single-species flocks. Unlike Snail Kites and Boat-tailed Grackles, Limpkins have long legs and often wade while foraging (Snyder and Snyder 1969). Thus, if "beating" offers an advantage to foraging in flocks, Limpkins are capable of forming their own single-species flocks, and unlike kites or grackles, would not need to rely on other species to disturb the substrate.

We can only speculate about why the use of beaters would have been used at this place and time, and not otherwise a common foraging strategy; although this behavior has been observed on a few occasions in other areas (e.g., Everglades National Park and Big Cypress National Preserve) since our original observations (M. Wilson, S. MacDonald, S. Dayhoff, pers. comm.; pers. obs.). Each time these flocks have been observed their dissipation has coincided with the time that Snail Kites, Boat-tailed Grackles, and Limpkins usually begin breeding in this area (January-February) (Sykes et al. 1995, pers. obs.). Consequently, the restricted mobility associated with breeding may have precluded persistence of these flocks. Water levels in these areas also were lower than those typically used, at least by nesting Snail Kites (Sykes et al. 1995), and sufficient water would have been unlikely to persist for the duration of breeding if nests had been initiated in the areas where these flocks formed.

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ROBERT E. BENNETTS, *Florida Cooperative Fish and Wildlife Research Unit, Univ. of Florida, Gainesville, Florida 32611*, AND VICTORIA J. DREITZ, *Dept. of Biology, Univ. of Miami, P.O. Box 249118, Corral Gables, Florida 33124.* *Received 20 Mar. 1996, accepted 1 Sept. 1996.*

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A description of nests and behavior of the Gray-headed Kite.—The Gray-headed Kite (*Leptodon cayanensis*), a little-known Neotropical raptor (Blake 1977, Brown and Amadon 1989, del Hoyo et al. 1994); occurs in lowland tropical forests from central-eastern Mexico to northern Argentina (Brown and Amadon 1989). Only one nest and two clutches of the species have been described (del Hoyo et al. 1994). Here, I describe three nesting attempts, one egg, and behavior of Gray-headed Kites in Tikal National Park, Guatemala during 1991 and 1993.

Study area and methods.—Tikal National Park (17°13′N, 89°36′W) is in a lowland, dry, semi-deciduous, tropical forest with an annual mean rainfall of 1348 mm (1989–1992, pers. obs.). Several forest types, which occur along topographical drainage, soil type, and moisture gradients (Schulze 1992) have been described for the park. Two extremes of this forest type continuum are upland or high-ground forests (tall, semi-evergreen forests on well-drained shallow soils) and the bajo forests (low in stature, open canopy with dense understory, and occurring in low-lying sites of deep clay-rich soils, subject to seasonal flooding and drought). Nest observations were made from ground level with 10× binoculars at distances of 35 to 50 m. Kites were caught with a noose carpet placed on the nest during incubation (see Newton 1986). Measurements (nearest 1.0 mm) were taken with a dial caliper and scale (Palmer 1962), and weight (nearest 1.0 g) was taken with a 1000-g Pesola spring balance. Kites were fitted with radio transmitters (Holohil Systems Ltd., Woodlawn, Ontario) which weighed 12 g (1.8–2.2% of body weight). Transmitters were attached to the birds by a backpack harness (Kenward 1987). Harness material was constructed of teflon tubing and flexible cable coated with rubber and secured by cotton thread and a crimped brass tube, respectively. A foam pad was attached to the base of the transmitter between the bird's back and the transmitter.

Results.—On 20 April 1991 I found a pair of Gray-headed Kites constructing a nest 24.4 m up in a 27 m palo de danto (*Vatairea lundellii*), (DBH 65.3 cm), in an area of transition from bajo forest to upland forest with emergent mahogany (*Swietenia macrophylla*) trees. The nest was loosely constructed of approximately 100 dried twigs and measured 40.0 cm in length by 33.0 cm in width and 8.0 cm deep. On 1 May, one of the kites was incubating. On 5 May, during 2.5 h of morning observations, I observed an incubation exchange between the two adults. The entering bird (sex unknown) uttered a soft cat-like "meow" call, flew in, and perched 5 m from the nest. The incubating bird stood, stretched, and made a weak chatter call to the perched bird, then flew south. The perched kite settled down on the nest to incubate. On May 9, I observed the nest from dawn (05:15) to dusk (18:30) MST. On my arrival, one kite was observed incubating. At noon a bird gave a feeble cat-like "meow" call from the east. Six minutes later a Gray-headed Kite entered the nest area, perched, then eight minutes later flew to the nest. The incubating bird then stood, stretched, and flew east out of view. The second bird settled on the nest and began incubating 2 min later. On May 18, I visited the nest from 05:30 to 07:30; on arrival there was a incubating bird on the nest. At 06:49 second kite approached with a dry twig and perched 5 m away from the nest. At 06:51 the incubating kite stood, stretched, and flew away. The second kite flew to the nest and placed the twig on it. By 07:05 the second bird began incubating. A single egg was in the nest on 21 May 1991. It measured 54.8 × 42.1 mm and weighed 49.0 g. The large end of the egg was a solid faded purplish brown that extended one-third the length; the other two-thirds were dirty white, spotted throughout with small rusty-brown spots.

On 21 May at 07:00, the incubating kite was trapped, measured, weighed, banded, radio tagged, and released. This bird returned immediately to continue nest duties. Several hours later the other pair member was trapped at the nest, measured, weighed, banded, radio tagged, and released. The first adult weighed 643 g. Its tail length was 261 mm, body length 521 mm, wing length 332 mm, hallux 23.2 mm, tarsus length 48 mm, middle toe 33 mm, and tarsus width 11.9 mm. I suspect this bird was a female because the weight was similar to those reported by Friedmann (1950), Blake (1977) and Brown and Amadon (1989) for females. The second Gray-headed Kite weighed 553 g, and its tail was 248 mm, body length 499 mm, wing length 321 mm, hallux 20.8 mm, tarsus length 48 mm, and tarsus width 8.4 mm. All these measurements are in the range of males reported by Friedmann (1950), Blake (1977), Brown and Amadon (1989). Both birds had blue-gray irises, gray-brown pupils,

gray-blue ceres, short, thick and heavily scaled toes, and blue-gray, scutellate, short, tarsi with thick scales. The bird believed to be the female had white underwing linings, while the presumptive male had black underwing linings.

On 28 May 1991, the adult thought to be the female was found dead below the nest. The bird had been plucked, and its breast and wing tissue were missing. Potential local predators included large raptors such as Ornate Hawk-Eagles (*Spizaetus ornatus*) and Crested Eagles (*Morphnus guianensis*). There was an occupied Ornate Hawk-Eagle nest 300 m NW of the kite nest. The egg was collected several days after this incident, when it became apparent that the male had abandoned the nest. The egg was deposited in the collection of the Western Foundation of Vertebrate Zoology (WFVZ 164,697).

A second nest containing a dead nestling was found on 3 July 1991, when an adult was observed leaving and returning to the same area several times within the forest. Another dead nestling was found on the ground at the base of the nest tree. The nest tree was a chicozapote (*Manilkara zapota*), 25 m tall and 88 cm DBH, located in an area of bajo forest. The nest was 22 m above the ground. Its construction was similar to the earlier nest. The white-downy nestlings had olive-yellow irises and yellow ceres and legs. Based on experience with similarly-sized raptors, I judged the nestlings to be approximately 2–3 weeks of age, as the mantle and flight feathers were just starting to emerge. The nestling on the ground was partially devoured. The nest measured 43 cm in length by 35 cm in width and was 7 cm deep. This nest and the first were 3.5 km apart, as determined through a Trimble Global Position System detector.

A third nest found on 20 April 1993 was 15 m west of a main road through Tikal National Park that continues to Uaxuctun, an archaeological ruin north of the park. The nest tree was a 28 m high palo de danto (*Vatairea lundellii*) 54.5 cm DBH located in a transitional forest. The nest was 26 m above ground. I checked the nest daily until the birds began incubating on 5 May 1993. The nest was poorly constructed; with the aid of binoculars, one egg could be seen through the gaps in the nest material. In late May a severe thunderstorm passed through the park and destroyed the nest. Measurements of the nest were not taken due to its damaged condition. The average dimensions of nest twigs (N = 10) were 38 cm by 0.5 cm. The nest was supported by five branches 25 cm, 5 cm, 4 cm, 2.5 cm, and 1.5 cm in diameter, respectively.

Aerial displays.—The dry season begins in February at Tikal National Park, and during this time Gray-headed Kites can often be seen giving unique courtship or territorial displays above the forest canopy. These distinctive displays consist of rapid shortened wing beats, in which in the wings are held above the horizontal plane after a soar or glide, a behavior I have termed the "butterfly display". A displaying kite broadcasts a ringing, hollow-sounding call. The call consists of a repeated note sounding like "caw," beginning slowly and accelerating rapidly, and lasting approximately three seconds. Another vocalization frequently heard is a two-note call that begins at a low frequency and shifts up the scale to a higher frequency second note.

Feeding observations.—Haverschimdt (1962) and Brown and Amadon (1989) reported that this species feeds on many different orders of insects and has a fondness for wasp larvae, but I did not observe any foraging on wasp nests during radio-tracking of a single kite. Gray-headed Kites have been observed feeding on cicadas flushed by marmosets (Ferrari 1990), but this foraging association was not observed at Tikal National Park between kites and primates. I observed one kite flying into a large mahogany tree and grasping at some type of prey, possibly a large cicada or a lizard that was resting on the outer portion of the tree, similar to the observation made by Haverschmidt (1962). Observations of the radio-tagged bird showed that hunting occurs in and below the canopy. This bird was observed flying from perch to perch in and below the canopy and scanning its surroundings

from the canopy down to the ground by moving its head slowly around. After several minutes, the kite typically flew to another perch and began searching again. Two weeks after radio attachment, the bird cut the surgical tubing and cable, enabling it to remove the transmitter. No prey captures were observed during the radio-tracking sessions.

Discussion.—The nesting observations reported here are the first for the Gray-headed Kite (*Leptodon cayanensis*) in Central America. My observations suggest that this species is not as rare at Tikal National Park as suggested by Beavers (1992). The nesting of Gray-headed Kites began in late April and early May, shortly before onset of the rainy season. Barlow et al. (1969) state that two female kites were collected in breeding condition in mid-April in British Honduras (Belize), and one contained an egg in the oviduct. All three attempts observed in this study involved nests that were structurally weak and positioned near the apex of canopy-level or emergent trees. This nest placement, typical of other kite species, may frequently lead to failures during intense storms and renders the nests vulnerable to other aerial predators (see also Snyder 1975). Although these three nesting attempts failed, I have seen several immature-plumaged Gray-headed Kites, including one that was following an adult from perch to perch in the park.

Clutches of two and three eggs were reported for two nests purportedly of this species by del Hoyo et al. (1994), but I found two nests containing one egg each and another containing two nestlings. Incubation exchanges were observed on three separate occasions, indicating that both adults participated in incubation. During my 13 h 15 min of observations at the first nest, the two adults were on the nest, incubating or resting, 44% and 56% of the time, respectively. This suggests that sexes probably incubate equally. No prey deliveries were observed at the nests during the incubation period, and I suspect that at this stage each non-incubating adult forages and feeds away from the nest. Haverschmidt (1962) reports he found in the stomachs of Gray-headed Kites only isopterans, hymenopterans, coleopterans, orthopterans, and larvae of lepidopterans, but later in the same paper he states that he found remnants of a frog and a bird's egg. The strong reptilian odor of the two trapped kites was characteristic of birds that frequently prey on snakes and lizards. The foot structure, with short, thick toes and heavy-scaled tarsi would appear to be good adaptations for taking reptilian prey. There is a strong correlation between this foot structure and reptilian prey as reported by (Bierregaard 1978).

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RUSSELL THORSTROM, *The Peregrine Fund, 566 West Flying Hawk Lane, Boise, Idaho.*
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Production of erythristic eggs by the Black-headed Gull in Poland.—Egg erythrism is rare and most records in gulls, terns, skuas, and lapwings involve only single cases (Bates et al. 1976, Hays and Parkes 1993). Only three cases have been documented in the Black-headed Gull (*Larus ridibundus*) (Jourdain and Borrer 1914 after Bates et al. 1976). In our study, erythrism occurred rarely but more often than reported for other species of gulls and terns (Bates et al. 1976, Sutherland 1980, Hays and Parkes 1993).

The objectives of this research were to quantify erythrism in colonies of the Black-headed Gulls and to compare the egg-laying phenology, nesting location, clutch size, and hatching success of females laying typical and erythristic eggs.

Study area and methods.—Study colonies were on islands in the Vistula (Wisla) River between Dęblin and Kozienice, Poland. In 1986, three colonies were studied and were near Pawłowice village (51°36′N, 21°40′E), near Kuźmy v. (51°38′N, 21°33′E) and near Kobylnica v. (51°40′N, 21°35′E) (Table 1). In the years 1987–1988, only the two latter colonies were studied, and in 1989–1990 only the Kobylnica colony was monitored. The river islands, in contrast to stagnant water, are not the typical breeding sites of Black-headed Gulls. This habitat has been occupied for a short time (Bukaciński and Bukacińska 1993). Monitored islands were overgrown by grass and/or willow and poplar shrubs with bare sandy sections.

TABLE 1

THE FREQUENCY OF THE OCCURRENCE OF CLUTCHES WITH ERYTHRISTIC EGGS IN DIFFERENT COLONIES OF BLACK-HEADED GULLS

	Pawłowice			Kuźmy			Kobylnica		
Year	N[a]	N[b]	%[c]	N[a]	N[b]	%[c]	N[a]	N[b]	%[c]
1986	160	1	<1.0	100	4	4.0	385	16	4.2
1987	—	—	—	800	0	0	200	12	6.0
1988	—	—	—	550	0	0	100	6	6.0
1989	—	—	—	—	—	—	1200	14	1.2
1990	—	—	—	—	—	—	70	4	5.7

[a] Number of all clutches monitored.
[b] Number of clutches with erythristic eggs.
[c] Percentage of erythristic clutches.

Gulls occupied both sandy beaches and sections highly overgrown with grass. Erythristic clutches were found in both habitats.

Nests were marked with sticks and checked every 3–5 days from laying of the first egg to hatching. Thirty pairs were trapped while incubating on nests and individually marked (including 7 with erythristic eggs) (Bukacińska and Bukaciński 1993). The hatching success was determined only for 30 from 57 clutches with erythristic eggs. The remaining 27 clutches were collected for analyses of pesticides content. For some statistical analyses the data for all years were combined. We used Students *t*-test and χ^2 test.

Results.—The ground color of a typical egg of the Black-headed Gull usually is green or olive, but only rarely brownish, with blotches variously distributed, ranging from dark green to brown (Makatsch 1974). The background of erythristic eggs of the Black-headed Gulls on the Vistula River ranged from buff-yellow and cream-coloured to light pinkish and always with a distinct reddish shade. There were a lot of almost black or brown blotches, often framed with violet. The distribution of markings was uneven. They were often concentrated at the large end, creating a kind of ring or cap. Sometimes the cap reached half of an eggs' length. The other half of the egg was either slightly blotched with violet or dark greyish or even without markings at all. Eggs of particular clutches differed both in intensity of background color and in the size and number of blotches. Some eggs had thin shells (shells were soft and cracked).

Most of erythristic clutches were found in the "Kobylnica" colony (Table 1). In 55.8% of them, all eggs were reddish in color. In the remaining clutches, most often only one egg was erythristic and the rest were typical. Nest location in the colony had no effect on the frequency of egg erythrism. We noticed the clutches with erythristic eggs in 2.9% (N = 40) of nests situated in the center of a colony and in 2.1% (N = 12) of the nests at the edge.

Clutches with erythristic eggs were laid more often at the beginning of the breeding season (χ^2 = 58.3, df = 5, $P < 0.0001$, Fig. 1). Forty-eight percent of the clutches with erythristic eggs were laid during the first five days of egg laying in a colony. Later in the season the occurrence of erythristic eggs gradually decreased (Fig. 1). This pattern of egg-laying differed from that of typical eggs (χ^2 = 52.4, 26.7 and 37.8, df = 4, $P < 0.001$, in the years 1986-88, respectively). During the first ten days, typical eggs were laid in only 10.3–12.3% of nests, and they peaked between 10–15 and 15–20 days from the beginning (Fig. 1).

Three egg clutches had the lowest incidence of egg erythrism, and one egg clutches the

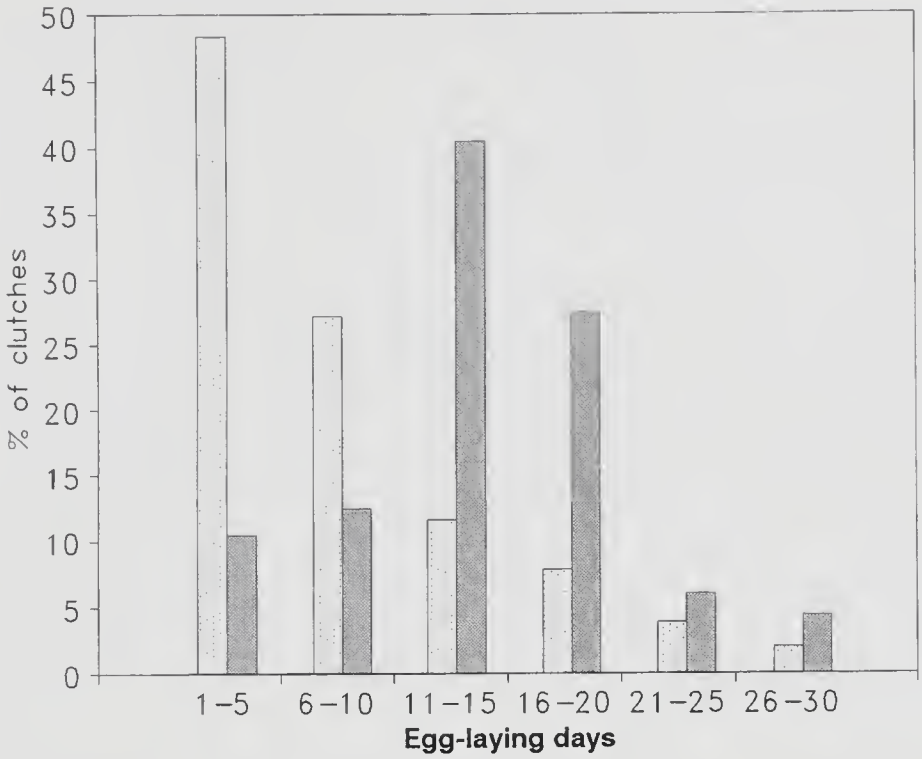

FIG. 1. Phenology of egg-laying in a Black-headed Gulls colony "Kobylnica" (time of laying first egg) in the years 1986–1990. OX axis "1" means the day of laying first egg in the colony. Dotted bars -erythristic clutches (N = 52), hatched bars—typical clutches (N = 494).

greatest (χ^2 = 60.5, df = 2, $P < 0.0001$) (Fig. 2). Clutches with erythristic eggs were smaller than clutches with typical eggs (t = 2.7, $P < 0.02$ and t = 2.0, $P < 0.05$ for 1986 and 1987, respectively) (Table 2).

Hatching success of clutches with erythristic eggs was lower than clutches with typical eggs (χ^2 = 5.7, $P < 0.02$ for 1986; Table 2). A higher percent of cracked eggs in erythristic clutches was the main cause of the lower hatchability (χ^2 = 23.7–166.3, $P < 0.0001$; Table 2), but even if cracked eggs were excluded from the analysis, the hatching success in erythristic clutches was still lower than clutches with typical eggs in 1988 (χ^2 = 4.2, $P < 0.05$).

Discussion.—Black-headed Gull colonies on islands of the Vistula River have a relatively high frequency (3% of nests, 57 clutches) of erythristic eggs compared to other studies (Bates et al. 1976, Sutherland 1980, Hays and Parkes 1993). The Vistula River is also the only place in Poland where that phenomenon has been reported. However, we do not know how to explain the high frequency of erythrism on the Vistula River.

The causes of laying erythristic eggs are unknown, although studies on Domestic Fowl (*Gallus gallus*) indicated that the color of eggs of individual females is genetically determined (Hutt 1949). Therefore it should be characteristic for individual females to lay similar eggs during their life. However, in colonies of the Black-headed Gulls we studied, only slightly more than half of the females that laid erythristic eggs laid clutches with all erythristic eggs.

Only two females (from seven individually marked) laid erythristic eggs every season. Three females that laid erythristic eggs laid typical eggs in successive years. We also found

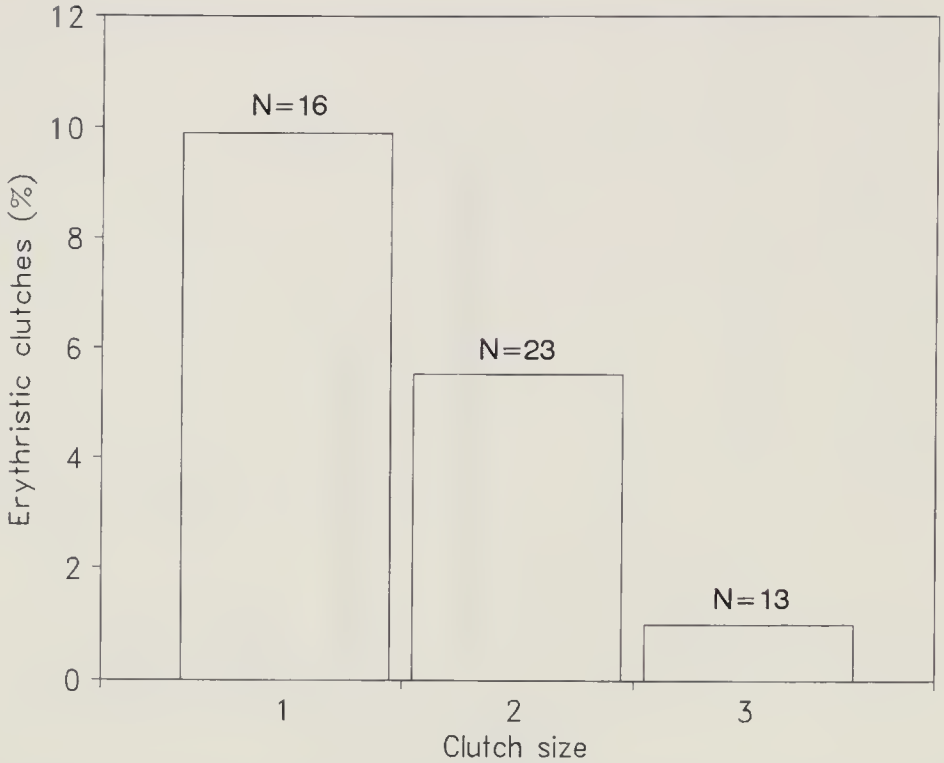

FIG. 2. The frequency of the occurrence of clutches with erythristic eggs within the clutches of different size.

TABLE 2

COMPARISON OF HATCHING SUCCESS OF ERYTHRISTIC AND TYPICAL CLUTCHES OF THE BLACK-HEADED GULL COLONY "KOBYLNICA" IN THE YEARS 1986–1988

Breeding parameters		Erythristic clutches	Typical clutches
Mean clutch size[a]	1986	1.86 ± 0.77 (14)	2.42 ± 0.14 (275)*
	1987	1.90 ± 0.74 (10)	2.37 ± 0.12 (192)*
	1988	2.16 ± 0.75 (6)	2.39 ± 0.11 (85)
Number of eggs laid	1986	26	660
	1987	19	463
	1988	13	184
Percent of cracked eggs[b]	1986	38.5 (10)	1.0 (5)**
	1987	52.6 (10)	1.5 (7)**
	1988	23.1 (3)	1.1 (2)
Percent of hatched eggs[b]	1986	34.6 (9)	54.8 (362)*
	1987	15.8 (3)	32.1 (151)
	1988	15.4 (2)	57.1 (105)

Number of nests or eggs given in parentheses.

[a] * $P < 0.05$, Student t-test.

[b] * $P < 0.05$, ** $P < 0.001$, χ^2 test.

the opposite situation -two females which had laid typical eggs in one year, laid erythristic ones in successive years. Mixed clutches of erythristic and typical eggs have been reported in two nests of the Glaucous Gull (*L. hyperboreus*) (Bates et al. 1976). Hays and Parkes (1993) reported one female Common Tern (*Sterna hirundo*) that laid erythristic eggs for four years and a typical one in the fifth. These cases suggest that the laying of erythristic eggs is not only genetically determined but that other factors affect whether they are laid, and how many in particular year (and successive).

Pesticides may be one of these factors. Recent unpublished studies of Łukowski et al. indicated increased level of pesticides in erythristic eggs. But the level was not high enough to change the color of eggs and cause the thickness of shell in large part of erythristic eggs (Table 2). The latter phenomenon was not described for erythristic eggs until now.

In poultry studies, there are viral diseases (IB: Avian Infections Bronchitis, EDS 76: Egg-drop-syndrome, Newcastle disease), bacterial diseases (Colibacteriosis), and fungal diseases (Mycotoxicosis) that result in periodic color abberations and changes of structure and thickness of the eggshell (Siegmann 1983, Borzemska et al. 1989). These diseases are also found in wild birds, including gulls (A. Kruszewicz pers. comm.). It may be that laying erythristic eggs is the result of both a genetic predisposition and condition of a female in a given year. This is supported by our results that show erythristic eggs are laid in smaller clutches and have a lower hatching success than typical eggs. The earlier time of laying of most of the erythristic eggs indicates they were laid by older birds which typically have large clutches and high success (Coulson and White 1958, Patterson 1965, Mills 1973, Ryder 1975). This could suggest that females laying erythristic eggs are not as healthy as females laying typical eggs (Coulson and White 1961, Winkler and Walters 1983).

In summary, we found that erythristic eggs were laid early in the season. The clutches were smaller with higher occurrence of cracked eggs and lower hatching success than typical clutches. All these indicate poor condition of females. However, we do not know all the factors which cause laying of erythristic eggs in a particular year. A more detailed study of marked females is necessary to help explain this phenomenon.

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DARIUSZ BUKACIŃSKI AND MONIKA BUKACIŃSKA, *Dept. of General Ecology, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny, 05-092 Łomianki, Poland.* *Received 13 Oct. 1995, accepted 20 Sept. 1996.*

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Variable plumage ontogeny in the Black (*Turdus infuscatus*) and Glossy-black robins (*T. serranus*).—Ontogenetic sequences and their relative timing are a major issue of interest in ornithology (Lawton and Lawton 1985, Thompson and Leu 1994) and biology in general (Gould 1977). Attention has focused on relative timing, social implications, and evolutionary transformations in the ontogeny of plumage and soft-part color characters. A detailed understanding of causes and trajectories of these changes may allow inferences regarding a variety of evolutionary processes (e.g., Peterson 1991a, b).

Recently, during efforts to inventory the vertebrate fauna of Cerro Piedra Larga, a remote, isolated 2850 m massif in eastern Oaxaca, Mexico, we had the opportunity to study and sample abundant populations of the local Black Robin (*Turdus infuscatus*). During a two-week study period (31 March–13 April 1993), we observed about 15 individuals daily, and collected 16 specimens for detailed plumage comparisons. This material, together with specimens examined in the collections of the Field Museum (FMNH), Natural History Museum of Univ. of Kansas (KUMNH), and the Museo de Zoología, Facultad de Ciencias, Univ. Nacional Autónoma de México (catalogued temporarily as OMVP), permitted us to document further a poorly known male plumage (Baepler 1962, Howell and Webb 1995) in certain populations of this species. Additional information on specimens was kindly provided by the Louisiana State Univ. Museum of Natural Science (LSUMNS).

The majority of the specimens collected on Cerro Piedra Larga were males in an all-black plumage with a yellow bill (8), or females in a uniform brown plumage with a dusky brown bill (5). However, three males (OMVP 279, 282, and 439) had female-like plumage, pneumatized crania (100%, 80%, and 100%, respectively), and gonads that were not minute (testes 3 × 5 mm, 3 × 5 mm, and 7 × 10 mm, respectively); only one (OMVP 279) showed any sign of molt, and that described as "some under tail," and hence not illustrative in direct determination of plumage sequences. These males were dusky-brown plumaged with occasional black feathers scattered over the body, and tended to have duskier colored bills than the yellow-billed adult males. On several occasions, we observed brown-plumaged

individuals actively singing and apparently defending territories, with songs indistinguishable from those of the black-plumaged males. Therefore, the Cerro Piedra Larga Black Robins appeared to have a subadult (predefinitive) female-like brown plumage before attaining the black definitive male plumage.

The subadult brown-male plumage is apparently present in many populations of the species. Specimens from San Luis Potosí (LSUMNS 12030, 12040), Oaxaca (KUNHM 45900, LSUMNS 3316), Chiapas (LSUMNS 41565), Guatemala (Baepler 1962), and El Salvador (FMNH 109817) all clearly indicated the existence of a brown plumage. Two specimens from Oaxaca (LSUMZ 33316) and Veracruz (FMNH 187377), Mexico, were apparently molting from the subadult brown plumage to the definitive black plumage. We found no molting specimens demonstrating the attainment of the subadult plumage from the juvenal plumage; however, several such specimens are in the collection of the Carnegie Museum of Natural History (K. C. Parkes, pers. comm.), documenting that this plumage is indeed the first prebasic plumage. No Middle American specimen indicated direct change from the juvenal plumage to a black plumage.

The Black Robin of Mesoamerica (Mexico south to Honduras) is sometimes considered conspecific with the disjunct Glossy-black Thrush (*T. serranus*) of the Andes of South America (Ripley 1964); conspecific or not, the two are at least closely related (AOU 1983). Several specimens of the latter species, however, indicated that ontogenetic variation in this species may be more complicated than in the Black Robin. Specimens from Venezuela (Sucre, Mt. Turuniquire, FMNH 92278-9) showed a clear brown plumage, one of which (FMNH 92278) was molting into the black plumage. However, specimens from Colombia (Popayan, Cauca, FMNH 282238) and Peru (LSUMNS 982083) were molting from the spotted juvenal plumage to a black plumage, suggesting direct transition to the black plumage without a brown subadult plumage. These and other specimens (LSUMNS 106514 and uncat.) suggest that the first plumage to replace the juvenal plumage, although blackish, may be more suffused with brown than subsequent plumages. Hence, ontogenetic sequences in the Glossy-black Thrush are complicated, and remain unclear based on specimens available.

Published documentation of strikingly delayed plumage maturation is surprisingly scant in the subfamily Turdinae. Three additional species that do show delayed plumage maturation are *Turdus merula* (Snow 1958), *T. olivater* (K. C. Parkes, pers. comm.), and *T. rufitorques* (Skutch 1960). Together with *T. infuscatus*, these examples seem few, given the size of the subfamily (179 species) and its near-cosmopolitan distribution. However, perusal of general references such as Cramp (1988) and Keith et al. (1992) suggests that this phenomenon exists in other species, at least of the Old World; and hence, delayed plumage maturation may not be as uncommon among thrushes as the literature might suggest.

Acknowledgments.—We thank our field companions for their assistance and interest during the field work on Cerro Piedra Larga, and the curators and staff of the Field Museum; Museo de Zoología, Facultad de Ciencias, UNAM; and Louisiana State Univ. Museum of Natural Science for access to specimens and information under their care. Thanks are due to Mark B. Robbins, Kenneth C. Parkes, Peter Stettenheim, Peter Pyle, and especially Christopher Thompson for comments on the manuscript. Financial support was provided by the National Science Foundation (DEB 92000863).

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GRISELDA ESCALONA-SEGURA AND A. TOWNSEND PETERSON, *Natural History Museum, The University of Kansas, Lawrence, Kansas 66045.* *Received 6 March 1996, accepted 30 Sept. 1996.*

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ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

Bird Life of Woodland and Forest. By Robert J. Fuller, illus. By Chris Rose. Cambridge University Press, Cambridge, England. 1995: 244pp. $64.95.—Chapter 1 provides a background to British woodland. Since World War II the acreage of woodland in Britain has increased from 6.7% in 1967 to 9.4% in 1980, much of it through increased planting of coniferous forest in Scotland. Despite much conversion of broadleaved woodland to conifer plantation, "ancient woods" (those that have existed continuously since 1600) still form 23% of all woodland in England. Distinct regional patterns in woodland in Britain persist: mixed deciduous woodlands with beech, hornbeam and sweet chestnut in the southeast; other mixed deciduous thence to Wales and central England; elsewhere upland sessile oak and birch woodland, with pine and birch woodland and birch and birch and hazel forests in Scotland. These regional patterns are the outcome of a long history of land management in Britain that has had significant effects on bird distribution, the subject of chapter 2. Here Fuller draws on the rich literature on European forests and their avifaunas to describe the historical pattern of bird distributional changes as forests declined. Some of the observations from his own work in the primeval Biálowieza forests of Poland will strike chords with students of tropical forests.

Chapter 3 turns to how birds use forests but essentially is a narrative description of seasonal changes in the composition and behavior of the bird assemblages present in woodland. American readers used to season-specific plot-oriented research accounts will be struck by the wealth of observational information available for all stages of the annual cycle of bird use of British woodlands. Chapter 4, although entitled "Abundance and distribution of woodland birds," is a systematic and largely quantitative treatment of determinants of bird abundance. A point of relevance to the current revival of the Clementsian versus Gleasonian debate is Fuller's baldly stated conclusion "There is no such thing as a 'typical woodland bird community'." This is the sort of statement one can make authoritatively only from decades of experience over the full spectrum of woodland types and is typical of Fuller's writing here. The chapter discusses such environmental influences as geography, altitude and land productivity in similar narrative accounts, but presents quantitative analysis in relation to woodland area. American ecologists may be surprised by Fuller's conclusion that there are few, if any, genuine forest interior species in European woodland, with the possible exception of the Capercaillie. Fuller concludes instead that birds are more often affected by area-independent attributes of woodland than by area-related ones. Americans inclined to dismiss Fuller's conclusion as peculiar to Europe might note his comments about the Lynch-Whigham demonstration that Maryland forest birds are more closely related to regulation characteristics than to forest area. Other issues addressed in this chapter include woodland isolation, edge effects, forest growth stage and patchiness, and stand structure.

The following four chapters focus in turn on specific woodland types, including scrub, broadleaved forests, upland forests, and coniferous woodland. In general these chapters introduce the type in general terms, discuss a set of examples of particular variants, discuss how birds relate to the specifics of the habitat type, and provide discussion of relevant woodland management issues. The role of grazing in woodland features more prominently than would be the case in an equivalent work on American forests, in part because of a long tradition of grazing livestock in wood pastures. Indeed Fuller makes a case for reinstating grazing in certain scrub habitats types that are losing crucial conservation features to vegetation outgrowth. Points of interest in broadleaved woods include continuing increase

in abundance of some species as woods age even beyond 100 years; the rich bird life of oakwoods in association with the enormous densities of defoliating caterpillars on oak trees; and the significance of beech mast in the population dynamics of certain species.

The final chapter discusses woodland and woodland birds in the context of the sweeping changes in the British countryside. Brief reviews of the effects of air pollution, climate change, recreation and disturbance, and farm woodlots are followed by a more extensive discussion of the significance of natural woodland for birds. In contrast to the United States, conservation effort in Britain has concentrated on issues of management of the remaining semi-natural woodland since the extensive tracts of forest still present in the U.S. have long since been lost from Britain. In an interesting parallel to the Wildlands proposal for North America, Fuller advocates creation of a new natural forest-large enough to simulate the dynamics of a wildwood "arguably the single most exciting development that could occur in British conservation." The book concludes with four appendices (the first two detailing the habitats and nest sites of British and (other) European woodland species, the third a useful glossary of terms in British woodland ecology and management, and the fourth a list of scientific names), an eighteen-page bibliography, and an adequate index.

The book is an excellent example of a genre of ecological writing still prevalent in Europe but uncommonly found in North America, one almost of natural history writing but without abandoning the rigor of ecology. One finds few statistical tests cited in Fuller's book but his quantitative examples have origins in a technical literature rooted in statistical testing or are rooted in a magnitude of personal experience that precludes serious challenge to his conclusions: the insights of weeks and months and years in the field permeate this book. Occasional shortcomings are evident; on page 66 one is told "see Fig. 5.3" but in another work, not very helpful if one doesn't have the work to hand! Fuller notes the importance of tree species richness for bird diversity but cites only some recent work, not Ulfstrand's pioneering demonstration of the relationship! We are told on page 75 that rhododendron woods are poor for breeding birds but do provide good roosting sites, and then meet almost *verbatim* repetition of the point six pages later. A penchant for statements such as "Pied Flycatcher is a surprising absentee from most birchwoods" (p. 117) without explanation as to why it is surprising is evident on several pages. However, I doubt it is possible to write a book without a few such slips getting through. A more substantive criticism is the emphasis on coppiced woodland: although close to Fuller's heart (he has authored multiple papers on this habitat), the habitat features here to an extent disproportionate to its overall importance for British woodland birds.

I suspect most of the North Americans who should read this book will not do so, with a chauvinistic "It's about British birds and North American birds are different" serving as justification. But in this attitude lies failure to learn from an international expert in the field. Fuller's systematic comparing and contrasting of the biology behind North American, British and European ideas about forest birds holds lessons worth considering. Most forest ornithologists should at least read this book in the interests of their general education; beyond that I expect that it will be in Europe that its real value will be evident.—RAYMOND J. O'CONNOR.

STOKES FIELD GUIDE TO BIRDS: EASTERN REGION. By Donald and Lillian Stokes. Little, Brown and Company, Boston. 1996: xxiv + 471 pp., numerous color photos and range maps. $16.95 (paper) and STOKES FIELD GUIDE TO BIRDS: WESTERN REGION. By Donald and Lillian Stokes. Little, Brown and Company, Boston. 1996: xxiv + 519 pp., numerous color photos and range maps. $16.95 (paper).—These photographic guides synthesize a tremen-

dous amount of information on the identification, behavior, habitat, and conservation of North American birds into a pair of field guides. The books are structured as species accounts with "learning pages" included before such difficult groups as hawks, shorebirds, gulls, flycatchers, warblers, and sparrows. For each species account, there are photographs, range maps, and sections pertaining to the identification, habitat, voice, conservation, feeding, nesting, and other behaviors of the species covered. The division of information into these standard sections makes information about a species easily accessible. While most species are covered on individual pages, a few species pairs are covered jointly, including the pairs of Cedar (*Bombycilla cedrorum*) and Bohemian waxwings (*B. garrulus*) and Northern (*Lanius excubitor*) and Loggerhead shrikes (*L. ludovicianus*). Both common and scientific names are up-to-date as of the fortieth supplement to the American Ornithologists' Union "Check-list of North American Birds" (Auk 112:819–830, 1995). The photographs are generally crisp and representative.

Several features of these books will be very attractive to beginning or novice bird watchers. One of the most innovative additions is the inclusion of symbols to indicate which species are likely to use bird feeders and/or bird houses. These symbols make it much easier for beginners to determine which species might be encountered in their yards or which species might be attracted with bird houses. Just prior to the species accounts is a "quick guide to the most common birds," which provides an even quicker guide to regular backyard birds. Additionally, color-coded tabs to bird groups make finding a group of birds much faster than flipping through the book or using the index.

Ornithologists and advanced bird watchers may find that these books have several deficiencies. For example, the guides do not adhere strictly to the taxonomic order outlined in the A.O.U. "Checklist of North American Birds" (6th ed., 1983). Scientific nomenclature is not available at the ordinal, familial, or subspecific level in these guides. Additionally, these guides are not as comprehensive as some of the available illustrated guides in their coverage of subspecific, sexual, and seasonal differences in plumages. Despite these deficiencies, these guides do provide an interesting and useful collection of information in a single, easy-to-use source and are certainly the best photographic field guides available.—SARA R. MORRIS.

BIRD CONSERVATION: THE SCIENCE AND THE ACTION. By John Coulson and Nicola J. Crockford (eds.) Ibis, 137: Supplement 1. 1995. 250 pp.—This volume is the proceedings of a meeting of 220 scientists and conservationists that took place in April 1994 at the annual conference of the British Ornithologists' Union in Bedfordshire, U.K. The goal of the conference was to bridge the gap between the science and action of bird conservation. The participants were from North America, Europe, Siberia, Australia, New Zealand, and South Africa. Representatives from South America, tropical Asia, and the rest of Africa were conspicuously absent.

The conclusions and recommendations are presented first as "a message to influence the role and direction of ornithology in conservation to the year 2000 and beyond." The important points are that if we are to succeed in our efforts to conserve birds, we must develop strong communicative partnerships between scientists and policy makers, develop international collaboration and resolve, make decisions based on sound science and grounded in a knowledge of natural history, pay attention to the landscape and the geographic region, monitor a wide species base, employ predictive models, manage intensively when there is little other choice, and evaluate critically the strategies and priorities for conservation.

The 34 contributions that follow the conclusions and recommendations range from brief

essays to detailed analyses and applications of models, reviews of hands-on management strategies, and extinction risk assessment. E. M. Nicholson begins with an interesting historical account of British ornithology and conservation and proposes future directions in research, management, outreach, and education. Next, Jeremy Greenwood et al. present a valuable assessment of new long term strategies for monitoring breeding birds in the United Kingdom, including an important discussion of statistical inference, power, and uncertainty. R. E. Green discusses the difficulties of detecting and diagnosing declines. Studies by Jesper Madsen on migratory waterfowl and David Gibbons et al. on Buzzards (*Buteo buteo*) and Ravens (*Corvus corax*) supply an important geographical perspective and call for the maintenance of the geographical ranges of native species.

The importance of a landscape perspective is emphasized by John Wiens in his insightful discussion of landscape mosaics and by H. Ronald Pulliam et al. in their use of mobile animal population (MAP) models. Paul Opdam et al. discuss metapopulations in landscapes, while Daniel Simberloff urges caution in attributing bird declines to changes in metapopulation dynamics.

Predictive models are used by many authors and are recognized as important tools in conservation, but only to the extent that they are grounded in knowledge of natural history and used in conjuction with long-term ecological research and monitoring. The importance of modeling density dependence, compensatory processes, and individual-based optimal foraging considerations is emphasized in many papers, like the particularly brilliant studies of Oystercatchers (*Haematopus ostralegus*) by John D. Goss-Custard et al. and of Grey Partridge (*Perdix perdix*) by G. R. Potts and Nicholas Aebischer.

Hands-on management of individual species is highlighted next, beginning with an overview by Tom Cade and Stanley Temple, and followed by individual papers on Nene (*Branta sandvicensis*), Mauritius Kestrel (*Falco punctatus*), and New Zealand flightless birds.

These papers are followed by a series of international perspectives on bird conservation from Siberia, the United States, Australia, and Europe. I was surprised that Partners in Flight is not mentioned. Conservation strategies for UK birds are elaborated further in papers on action plans, priorities, and the role of statutory bodies. The volume ends with a global view of conservation priorities by Colin Bibby and an assessment of the meeting by Staffan Ulfstrand.

This publication, with its wealth of information on a diverse array of topics related to bird conservation, will prove to be a valuable resource for scientists, conservationists, and upper-level students of conservation biology and ornithology. It establishes a strong foundation from which to build strategies for conservation research and monitoring, and for turning science into action.—David C. Morimoto.

The Wind Masters: the Lives of North American Birds of Prey. By Pete Dunne, illus. by David Sibley. Houghton Mifflin Co., Boston. 1995: 263 pp., 66 black-and-white drawings. $22.95 (cloth).—This book consists of 33 short stories—one each about thirty North American diurnal raptors (hawks) and three New World vultures. They present a brief glimpse into the lives of fictional representatives of each species, a snapshot in time used by the author to say something instructional about each. The author states in his introduction that he has chosen fiction as a vehicle because of the "effectiveness of this writing technique as an instructional tool." Dunne's great writing skills and profound appreciation and breadth of knowledge of raptors have enabled him to make this rather iconoclastic approach pay big dividends. I found the imagery and metaphor delightful, e.g., a hawk "tearing pieces of Red-winged Blackbird free with her bill and offering a tribute of feathers to her ally the

wind," or vultures "Huddled on their perches, wrapped in shabby vestments, the birds look like a group of balding monks gathered in prayer." I am usually offended by blatant anthropomorphism in instructional writing, but found a magnanimous eagle, a vulture "hissing a few bars of 'Teddy Bear's Picnic'", or a condor dreaming rather appealing. The stories *are* instructional—they contain loads of information on raptor biology, and each species has clearly been thoroughly researched. An evolutionary theme is present throughout, along with philosophical abstractions and speculations involving predator/prey relationships and human interactions. When it comes to human interactions, Dunne is careful to distinguish between hunters and hawk shooters: "Hunters are conservationists who admire and are supportive of the creatures they hunt . . . Hawk shooters are ignorant, selfish bastards who like to kill things."

The book follows a progression of seasons from one winter through the next, and each species has been used to focus on some aspect of raptor biology (e.g., courtship, fledging, migration) through this sequence of seasons. The last chapter (story) deals with the California Condor (*Gymnogyps californianus*), and Dunne presents a history of this species' decline and thoughtfully defends the recovery efforts.

The book is beautifully illustrated by David Sibley with a portrait profile cameo to begin each chapter and a full-page drawing depicting some situation described in the story.

This is a marvelous book, a compendium of wonderful, poignant, informative, and thought-provoking stories. I cannot imagine anyone not wanting to read them.—WILLIAM E. DAVIS, JR.

NATURAL HISTORY OF THE UNICOLORED JAY IN CHIAPAS, MEXICO. By Tom Webber and Jerram L. Brown. Proceedings of the Western Foundation of Vertebrate Zoology 5: 135–160 Camarillo, California. 1994: four numbered text figures, 11 tables. $5.00 (paper).—Unlike its congeners, the Mexican Jay (*Aphelocoma ultramarina*) and Scrub Jay (*A. coerulescens*), little is known about the behavior and ecology of the Unicolored Jay (*A. unicolor*) which lives in mountain forests from central Mexico south to El Salvador. This remarkable pioneering study of the social system of a tropical forest species was conducted in the mountains of southeastern Chiapas, Mexico, along the Guatemalan border.

About half the birds in each of four groups were marked with flexible, colored plastic leg flags and matching bands. In two groups, the two unbanded birds could be distinguished by plumage patterns. Incubation and care of the young were observed from 0700 to 1200 daily, weather permitting. Observation of fledglings was more variable because of the difficulty of finding and following the birds. Sex of some birds was inferred from their role in incubation and brooding, by their copulatory and mate-guarding behavior, and whether or not they gave the "Rattle" call, which is given only by females in congeneric species of jays. Such use of multiple behavioral criteria was found to be more reliable than use of weight and wing length which showed no sex differences.

Unicolored Jays live in groups of 4-9 birds ($\bar{x}$ = 6.5, N = 6) one year old or older that defend an all-purpose territory of about 30 ha which is defined by the local topography. The group includes one breeding female, who is two or more years old, and one or more non-breeding females, also one primary male and one or more secondary males. Membership of the groups was stable throughout the study, but members often separated into smaller, temporary groups, which reassembled after variable intervals.

The omnivorous jays foraged in the canopy. They also stored and retrieved plant food, some of which looked weathered, suggesting prolonged storage and the ability to remember the location of such items. Intrusions of neighboring groups were repulsed when all members

of the group confronted the intruders with calls and display flights past the opponents. Although no predation was observed, the jays mobbed, chased, attacked, and gave alarm calls to a variety of birds and mammals including potential predators.

Displays of Unicolor Jays were similar to those of congeners and included song displays, variations on begging, allofeeding which was common, and allopreening which was rare and brief. All members of the group except the dominant male were fed by one or more other members of the group, which leads the authors to suggest that allofeeding is important to group cohesion. Copulation was usually at the nest and not preceded by elaborate display. The concentration of display behavior between the beginning of nest construction and the beginning of incubation seems to reflect courtship and mate-guarding by the dominant male, attempts by subordinate males to court and copulate with the primary female, and attempts by subordinates to pair. In fact subordinate males that fed the primary female also followed her when she was away from the partially constructed nest and appeared to copulate with her, but as the nest neared completion the primary male followed the primary female more closely and kept subordinate males away. Could a subordinate male father some of the nestlings? Possibly, but DNA will be difficult to obtain and such analysis was not part of this study. Subordinates did copulate occasionally, but there is no evidence that subordinate females contributed to the clutch. Again, one wishes for DNA evidence. The behavioral differences among group members, between successive reproductive attempts within a group, and among the groups raise many unanswered questions concerning the social dynamics of the Unicolored Jay.

The nest is a typical corvid nest of sticks 5.5–13.5 m up in an oak. The primary male and female provide most of the nest material, although other group members contribute some. Only the primary female incubates and broods. She is fed by all group members. The three to four nestlings remain in the nest 21–26 d and are fed by most or all group members. Once out of the nest, the fledglings are fed by most of the group members. In both the nestling and fledgling stages the primary female is the least likely to feed the young, whereas the primary and secondary males had about equal feeding rates.

How do Unicolored Jays compare to their better studied congeners? Group size is intermediate between that of the Scrub Jay and Mexican Jay. Like the Scrub Jay, only one female breeds per group. Like the Mexican Jay, more than one male may copulate with and fertilize the primary female, and most or all members of the group feed the young. Unlike both congeners, all members of the group participate in nest construction.

Comparative study is the cornerstone on which our understanding of behavioral function and phylogeny rests. This comparative study is important as an addition to the literature on the social behavior of jays and as a pioneering study of the social behavior of a tropical forest species.—EDWARD H. BURTT, JR.

A BIRDER'S GUIDE TO EASTERN MASSACHUSETTS. By Bird Observer, illust. by Barry W. Van Dusen. American Birding Assoc., Inc., Colorado Springs, CO. 1994. 304 pp. maps and bar graphs. $14.95 (paper).—Many birders traveling to an unknown territory on a birding trip rely on the birdfinding guides available through the American Birding Association to locate areas in which specialties may occur. These guides, formerly known as the Lane Guides, have concise directions and detailed maps. The newer volumes are spiral-bound and are of a size that is easy to carry.

This recently published guide for Eastern Massachusetts is no exception. It is a compilation of site guides that have appeared in *Bird Observer* since its inception in the early '70s, and a wealth of additional information. Although there are a number of contributing

authors, the writing is in much the same vein, making the book very readable. The guide was well planned with a quick reference map on the inside back cover. The detailed maps are excellent and, for the most part, very easy to read. The section relating to specialties and the bar graphs are informative. There are special sections on pelagic birding, both on land and by sea, and spring and fall hawk watching.

One's initial reaction to this book might ask, why the Massachusetts guide is as thick as some for the large western states (and it only covers the eastern two-thirds of the state at that). Most birders have heard of Newburyport (first site of Ross's Gull in the lower 48) or Monomoy Island off Cape Cod, but the distant birder may not have heard of the many other good birding spots. One can spend days or even weeks and still never cover all the places detailed in the guide. From Salisbury Beach to Provincetown, Martha's Vineyard, and Nantucket, from Mt. Auburn Cemetery in Cambridge, to Quabbin Reservoir, there is something for birders at every level.

Massachusetts, for its size, has been blessed with a large diversity of habitat that attracts birds in great numbers depending on the season and the weather conditions. The areas and best times to visit are well described in this guide. The waters off Massachusetts provide some of the best pelagic birding on the east coast, and this guide details both where and when to see both birds and mammals. There is a listing of the various whale-watching boats, as well as organizations that sponsor trips strictly to see birds.

The chapter on hawkwatching covers the best sites and times for viewing the largest number of hawks and also provides an overall view of hawkwatching in the northeast.

When planning to visit a specific area, a birder would be wise to consult the guide ahead of time for problems that might be encountered, such as congested urban areas, missing street signs, or the best time of day to visit. Be sure to obtain a tide table when planning to bird along the coast.

There are numerous notes throughout the book regarding private property and using good birding ethics. It is important that birders follow these guidelines.

My only disappointment in the book is that it does not cover several excellent birding places in the western part of the state, including Mt. Greylock. Will there be an addendum to this guide some day that will cover the rest of the state?

If you are heading for Massachusetts on a business trip, off to visit the historic sites of this great state, or planning a birding trip to the northeast, be sure to take this book along—I highly recommend it.—Betty S. Kleiner.

Ecology and Conservation of the Marbled Murrelet. Edited by C. John Ralph, George L. Hunt Jr., Martin G. Raphael, and John F. Piatt. Gen. Tech. Rep. PSW-GTR-152, Albany, California: Pacific Southwest Research Station, U.S. Dept. of Agriculture, Forest Service, P.O. Box 245, Berkeley, California 94701-0245. 1995: 420 pp., 35 maps, 103 tables and 104 figures. Free (paper).—This substantial volume (mass 1.4 kg) sheds considerable light on the enigmatic forest-nesting seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). This species is confined to a narrow strip along the Pacific coast of the United States and Canada, from the Aleutian Islands to California (an additional [sub] species is found in Russia and Japan). Generally seen inshore, its range may extend seaward 40 km and inland for 70 km where suitable nesting habitat exists. Concern for its status surfaced notably in the 1980's with resolutions from the Pacific Seabird Group and, later, the National Audubon Society. These eventually led in 1992 to a formal Federal listing as threatened for the populations in Washington, Oregon, and California. The species had been designated as threatened in Canada in 1990. The resulting assessments of the species' populations are

summarized in this volume and include information gathered through the 1993 breeding season. The assessments apparently were used in development of the Draft Recovery Plan (published by the U.S. Fish and Wildlife Service in July 1995). Four of the six members of the Recovery Team are among the authors of one or more chapters in the Assessment.

The book contains 37 chapters (ranging in length from 2 to 23 pages) by 45 authors, and a single section listing nearly a thousand references. The chapters are each structured like traditional scientific papers, and the authors seem to have been under a firm editorial hand. The absence of a subject index impedes some uses of the volume. The introductory chapter (by the editors) provides a clear overview of the species' status and of the results of this interim assessment which addressed the reasons for listing. These were primarily the loss of old growth forests (nesting habitat) and, secondarily, losses at sea due to net fisheries and the potential threat of oil spills. Following the two introductory chapters the book is divided into four parts: nesting ecology, biology and behavior (7 chapters), terrestrial environment (activity patterns and habitat use) (11 chapters); the marine environment (foraging, threats and distribution) (15 chapters); and two chapters on trends and status of population and habitat. Inland surveys and work at breeding sites posed formidable difficulties, even for establishing baseline data on this secretive bird. Although more readily observed at sea, the numbers are difficult to interpret. For instance, one estimate of the Oregon population is three times another. Preliminary analyses of productivity, based on adult/young ratios at sea, suggest that the present populations would continue to decline for some time, even without further loss of habitat, because displaced breeders are not replacing themselves. However, considerable uncertainty remains about year-to-year variations, and most demographic features are poorly known.

Several research needs are identified, notably relating to nest predation (especially by corvids) in the fragmented forests. Some of these needs, and the tentative nature of some conclusions, will have been addressed in subsequent work. The inventories and methods developed here can be the bases for monitoring and for analytical studies. Despite an overall somber tone to the conclusions, it is encouraging that the editors remain optimistic about the long-term survivability of the species throughout its range. It is to be hoped that the accumulated knowledge will be wisely used, not only for the populations currently listed, but also in southeastern Alaska where the largest numbers of Marbled Murrelets are now facing massive impacts.—JEREMY J. HATCH.

LIFE ON THE EDGE: A GUIDE TO CALIFORNIA'S ENDANGERED NATURAL RESOURCES. Carl G. Thelander, Ed. BioSystems Books, Santa Cruz, California. 1994. 550 pp., numerous color plates and photographs. $45.00 (paper).—This multiauthored, lavishly illustrated, coffee table sized volume is designed to provide a layman's introduction to the natural history of 115 of California's endangered or threatened species. Of the 512 text pages, 123 are devoted entirely to birds. Twenty-nine bird species and subspecies are discussed, including the California Brown Pelican (*Pelecanus occidentalis californicus*), Light-footed Clapper Rail (*Rallus longirostris levipes*), Marbled Murrelet (*Brachyramphus m. marmoratus*), Willow Flycatcher (*Empidonax traillii*), Bank Swallow (*Riparia riparia*), San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*), and Inyo California Towhee (*Pipilo crissalis eremophilus*). The individual species accounts which comprise most of the book include brief, overviews of basic biology, conservation and recovery efforts, and other relevant information. Included with each species account is a map showing current breeding and wintering range in California. All species are illustrated in color, often several times. Species accounts are not generalized but are specific to the species' natural history in California. Adding a

somewhat eclectic component to the work, interspersed among the species accounts are essays dealing with historical or anthropological matters. For example, included among the bird accounts is "Why the humming-bird became eagle: legend from the Santa Rosa Indian Reservation."

This book succeeds in its objective of providing an attractive and useful introduction not only to California's threatened and endangered species but of also providing some context for the reader to comprehend how the state has changed historically and how change continues to effect the status of species. Anyone with a serious interest in California natural history will probably find much enjoyment in reading this book. Included is a complete authors list, index, glossary, and appendix listing additional species and subspecies of concern (39 of which are birds) and showing in which counties (there are 57) each of those listed occurs. The literature cited section is brief and highly selective.—JOHN C. KRICHER.

HANDBOOK OF THE BIRDS OF THE WORLD. VOLUME 2: NEW WORLD VULTURES TO GUINEAFOWL. By J. del Hoyo, A. Alliott and Jordi Sargatal (eds.). Lynx Edicions, Barcelona, Spain. 1994:638 pp., 60 color plates, $75.—This is the second volume in this monumental series. The quality of the work remains high—the text is excellent and thoroughly clear. The small print will tax the vision of some readers, but is clean and relatively free of typographical error. The illustrations are attractive and clean, although the range of plumages occuring in some species is not shown (e.g., Bald Eagle [*Haliaeetus leucocephalus*]). Given the size of the text, the price is well within reason. However, it is a pity that the costs of the series (more than $100 per volume for a total of 12 volumes) will prohibit acquisition by all but libraries, the very dedicated, or those with lots of surplus cash—C. R. BLEM.

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Editor Charles R. Blem
Department of Biology
Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

Editorial Board Kathy G. Beal
Richard N. Conner
Thomas M. Haggerty
John A. Smallwood

Review Editor William E. Davis, Jr.
127 East Street
Foxboro, Massachusetts 02035

Assistant Editors Leann Blem
Albert E. Conway

Index Editor Kathy G. Beal
616 Xenia Avenue
Yellow Springs, Ohio 45387

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Membership inquiries should be sent to Dr. John Smallwood, Dept. of Biology, Montclair State Univ., Upper Montclair, New Jersey 07043.

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POPULATION DECLINES OF THE PUERTO RICAN VIREO IN GUÁNICA FOREST

JOHN FAABORG,[1] KATE M. DUGGER,[2] WAYNE J. ARENDT,[3] BETHANY L. WOODWORTH,[4] AND MICHAEL E. BALTZ[1]

ABSTRACT.—Abundance of the Puerto Rican Vireo (*Vireo latimeri*) in Guánica Forest, Puerto Rico, has declined gradually over the period 1973–1996 as determined by constant-effort mist netting. Concurrent studies of breeding vireos show low nesting success, primarily due to parasitism by Shiny Cowbirds (*Molothrus bonariensis*). This decline may reflect the rather recent entry of the cowbird into Guánica Forest during the breeding season, as other factors (vegetation change, rainfall) do not seem to explain the decline. As a single-island endemic, it is important that the cause of this decline be determined so that recovery efforts can begin while the species is still moderately abundant. *Received 7 May 1996, accepted 10 Oct. 1996.*

We have monitored birds in Guánica Forest, Puerto Rico, since 1973, first with a single mist net line (1973–1996), then with multiple lines (1989–1996). Here we present evidence of a decline in abundance and possible declining survival rate of the Puerto Rican Vireo (*Vireo latimeri*) during the period 1973–1996. These patterns may be explained in part by the low reproductive success which has been found in this species in recent years, primarily due to parasitism by the introduced Shiny Cowbird (*Molothrus bonariensis*; Woodworth 1995). We discuss the possible factors causing these declines in this forest. Because the Shiny Cowbird has become widespread on the island only in recent years, we feel these trends may reflect island-wide declines of this single-island endemic.

[1] Division of Biological Sciences, Univ. of Missouri, Columbia, Missouri 65211.
[2] School of Natural Resources, Univ. of Missouri, Columbia, Missouri 65211.
[3] International Institute of Tropical Forestry, P.O. Box B, Palmer, Puerto Rico 00721.
[4] Dept. of Ecology, Evolution and Behavior, Univ. of Minnesota, St. Paul, Minnesota 55455.

STUDY AREA AND METHODS

The Guánica Forest of southwestern Puerto Rico is a 4000-ha reserve comprised of subtropical deciduous forest on a limestone substrate (see Terborgh and Faaborg 1973 for a detailed description with photographs). It has been protected for over 60 years by the Commonwealth of Puerto Rico and is designated a United Nations Biosphere Reserve. About half of the reserve has relatively undisturbed forest, while the remainder is 60-year-old or older second growth.

Monitoring of bird populations has been done for 23 years using lines of mist nets operated from dawn to dark for three consecutive days (Terborgh and Faaborg 1973, Faaborg, in press) in January or early February. A single line of 16 nets (each 12 m long, 36 mm mesh, 2.6 m high) strung end-to-end has been operated annually since 1973 (except 1977 and 1979). In 1989, more intensive netting was begun, with a total of seven 16-net lines in 1989, an additional line added in 1990, and another line in 1991, resulting in nine lines during 1991–1996. Lines are run in the exact location each year, such that we have one 23-year sample, six eight-year samples, one seven-year sample, and one six-year sample. Because capture rates are low by the third day, we feel these constant-effort samples provide a good index of relative population size when compared from year to year. Here, we report total captures of vireos by net line for the three-day sampling periods.

The Puerto Rican Vireo is well suited to population monitoring and survival estimation by use of mist nets. It forages in thick vegetation within the height of the nets (<2.5 m; Cruz and Delannoy 1984), so it is easy to capture with regularity. Vireos are territorial throughout the year, show low dispersal rates from territories, and have high potential longevity (as high as 13 years, 2 months; Woodworth 1995). Territories are approximately 200 m across (Woodworth, unpub. data), so one to three territories could overlap one net line. The net lines provide independent samples, as a vireo has never been caught in two lines within the same year. Given these traits and the fact that a single species is involved, we feel we have avoided all the problems associated with mist-net capture data as discussed by Remsen and Good (1996).

All birds captured were banded and immediately released, with recaptures recorded over time. We recorded the net in which captures took place in order to determine dispersal and territorial behavior. These recapture data allowed us to estimate survival rates using the program JOLLY (Pollock et al. 1990). We compared survival estimates of Puerto Rican Vireos for the following time periods and sample efforts: the single, original net line for 17 years (1973–1990; Faaborg and Arendt 1995), the single, original net line for 23 years (1973–1996), and eight new net lines for seven years (1989–1996).

The appropriate model was selected for each of these data sets using Chi-square goodness-of-fit tests and likelihood ratio tests between models whenever possible (Pollock et al. 1990). Models that generated estimates with the lowest coefficients of variation were chosen when there was insufficient data to perform goodness-of-fit tests. Model D, which assumes constant survival and capture probabilities, provided the best estimates of survival for the original line during 1973–1990 (Faaborg and Arendt 1995) and during 1973–1996. Model B, which assumes constant survival rates and time-dependent capture probabilities, provided the best estimates for the new lines during 1989–1996.

RESULTS

All of the measures of total captures or capture rates for the Puerto Rican Vireo for the period 1973 to 1996 suggest declining populations. The original net line never caught more than four individuals per sample

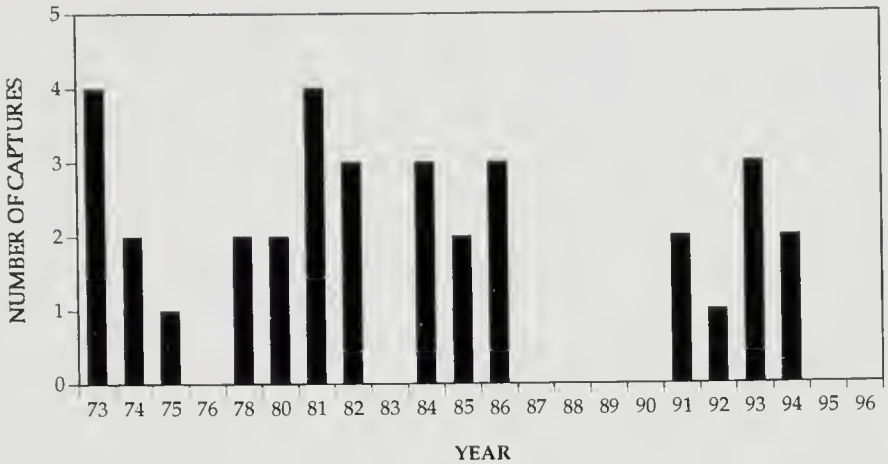

FIG. 1. Captures of Puerto Rican Vireos on the original Guánica net line during 1973–1996.

(Fig. 1), but the occurrence of no captures in six of the past 10 years (in contrast to two of the first 12 samples) suggests a local population decline. A regression of these data suggests about a 5% annual decline ($y = -0.0673x + 7.2748$; $R^2 = 0.1155$). The seven net lines that have been operated annually for the period 1989–1996 show a decline from 27 total captures in 1989 to as low as eight captures in 1995 (Fig. 2). While there was a slight increase in captures in 1996 (10), it is interesting to note that

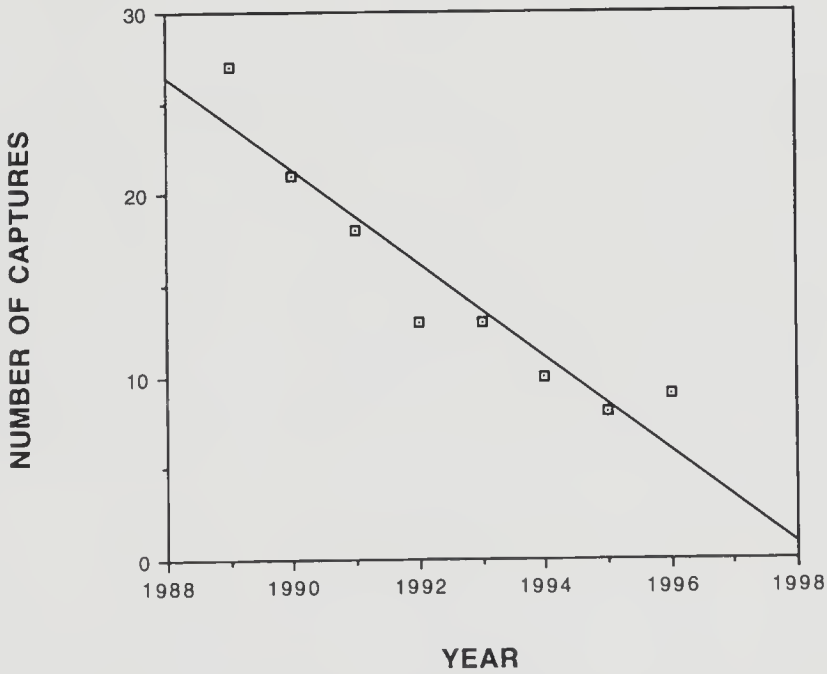

FIG. 2. Total captures of Puerto Rican Vireos annually on the seven net lines operated during the period 1989–1996 ($Y = 2.5595X + 5114.7$; $R^2 = 0.8966$).

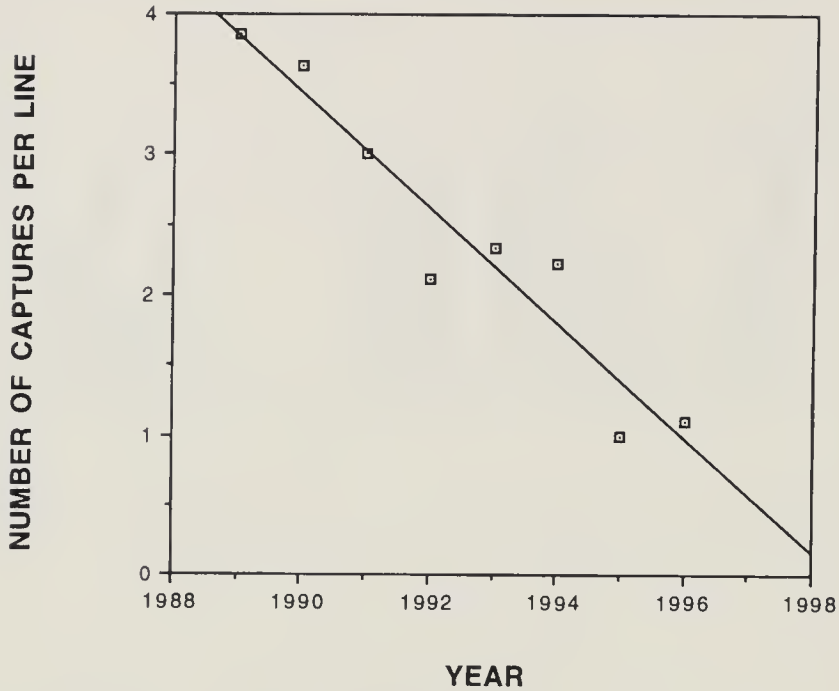

FIG. 3. Capture rates of Puerto Rican Vireos measured as mean vireos captured per net line for all net lines operated during the period 1989–1996 ($Y = 0.4101X + 819.57$; $R^2 = 0.915$).

nine of these birds were recaptures of birds banded in prior years. Mean captures per net line (for seven, eight, or nine lines annually) also shows a marked decline during 1989–1996, with nearly four birds caught per netline in 1989 and less than one in 1995 (Fig. 3).

Our estimates of annual survival for Puerto Rican Vireos have declined somewhat since the beginning of this study, although differences are not statistically significant. This trend is strongest for the birds captured in the original net line, with survival rate estimates declining from 0.68 (±0.08; Faaborg and Arendt 1995) during 1973–1990, to 0.61 (±0.08) when six more years of recapture data were added (1973–1996). During 1989–1996, survival estimates for the new lines were 0.63 (±0.06). An analysis done after the 1994 banding season suggested severe declines in annual survival rates (0.54 ± 0.06), but during 1995 and 1996 we captured four individuals which had not been seen for three to six years, which raised the survival rate estimate.

DISCUSSION

The results from intensive mist netting suggest that the population of Puerto Rican Vireos in Guánica Forest declined during the period 1973 to 1996, with evidence for a forest-wide decline during 1989–1996. Furthermore, estimates of survival rates suggest that mortality or emigration

has increased in recent years. The decline in numbers of vireos may be the result of a decline in reproductive success due to increased brood parasitism rates, increased predation, or environmental factors. The Shiny Cowbird, a generalist avian brood parasite, first arrived in northeastern Puerto Rico in 1955 (Grayce 1957). A study of reproduction by the Puerto Rican Vireo during 1990–1993 has documented low reproductive success in this species (Woodworth 1995), primarily due to parasitism by the introduced cowbird. Of 98 active nests, 83% were parasitized, and parasitism decreased vireo reproductive success by 82%. Only 5% of active nests fledged vireo young. Breeding pairs made as many as six nesting attempts per season, resulting in only 0.24–1.33 vireo young per female per year. Population models show that prior to the cowbird's arrival in Guánica Forest, this population of Puerto Rican Vireos was probably growing or stable, but that currently the population is not producing enough young to replace adult mortality (Woodworth 1995). An increase in nest predation rates might also cause such a decline. However, most Puerto Rican Vireo nest predation events in Guánica were caused by avian predators (Woodworth 1995), and there is no evidence that numbers of avian nest predators in Guánica have increased over the time scale of the mist netting study (Faaborg and Arendt, unpub. data). Furthermore, population models have shown that even with the current predation rates, an unparasitized population would sustain itself (Woodworth 1995). Finally, environmental factors can affect fecundity. Faaborg and Arendt (1992) have shown fairly large fluctuations in populations as a result of rainfall variation since 1973, but the recent period has not shown either severe drought or hurricanes. In addition, insectivorous birds are generally least affected by drought, and other insectivores (such as the Puerto Rican Flycatcher (*Myiarchus antillarum*) and Adelaide's Warbler (*Dendroica adelaidae*)) did not show declines during this period.

A decline in numbers of vireos might also be caused by an increase in adult mortality or emigration. In open population models, death and permanent emigration are indistinguishable (Pollock et al. 1990), although in either case, the absence of vireos from previously occupied territories supports a population decline. As discussed above, there is no evidence that survival during this period was affected adversely by drought or hurricanes. Predation on adults appears to be relatively low; in only two of 98 active nesting attempts (with over 900 exposure days) was the incubating adult taken by a predator. Female songbirds are more likely than males to disperse, particularly following nest predation (Jackson et al. 1989). Thus, permanent, or at least long-term, emigration may be a female's response to nest predation or nest failure due to cowbird parasitism. On the other hand, the energetics of building as many as six nests

and laying multiple clutches may lead to increased mortality in Puerto Rican Vireo females, as has been suggested in the Black-capped Vireo (*Vireo atricapillus*; Gryzbowski 1995).

The steepness of the observed population decline in the 1990s could reflect increased mortality, as birds that maintained populations in the 1980s reached maximum age, or there may be an emigration component at work. It is also likely to be due to an increase in the local cowbird population. Censuses and net lines operated in the study sites during the breeding season in the late 1960s and early 1970s rarely recorded cowbirds (Faaborg 1980, Kepler and Kepler 1970), although they occurred elsewhere on the island (Wiley 1985, Perez-Rivera 1986). Seven censuses in Guánica Forest conducted during the breeding season of 1969 detected only four Shiny Cowbirds in 672 km of trail (Kepler and Kepler 1970). A net line operated in July of 1981 caught no cowbirds, and only a single bird was observed during a visit in June of 1983 and in a net line in winter of 1988. In contrast, cowbirds are now common during the breeding season, as Shiny Cowbirds were detected at 27% of 176 unlimited-radius point counts conducted throughout the forest during the 1993 breeding season (Woodworth 1995).

The breeding status of the Puerto Rican Vireo outside of Guánica is not well known. Although it occurs throughout much of the island, occupying forests and brushy pastures (Raffaele 1989), so does the Shiny Cowbird. Data from an ongoing study in successional pastures in and around Cabo Rojo National Wildlife Refuge (CRNWR) suggest that Puerto Rican Vireos may also be in trouble outside of Guánica. In over 2000 h of mist netting in the CRNWR, we have captured only one Puerto Rican Vireo, whereas in similar habitat nearby, in an area known as Pitahaya, we have had capture rates of Puerto Rican Vireos similar to those found in Guánica in the early 1970s (3 per net line). One factor that may account for this difference is extensive Shiny Cowbird eradication efforts in the Pitahaya area as part of ongoing efforts to save the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*).

More information on reproductive success of vireos in other habitats needs to be gathered to see if this population collapse is island wide or confined only to Guánica. Although vireo populations appear to be declining in Guánica Forest, there are still many vireos present, so there is time to evaluate the problem and determine what can reverse these current trends.

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RED-COCKADED WOODPECKER FORAGING ECOLOGY IN AN OLD-GROWTH LONGLEAF PINE FOREST

R. Todd Engstrom[1] and Felicia J. Sanders[1]

Abstract.—Most Red-cockaded Woodpecker (*Picoides borealis*) populations are in pine forests that have been harvested at least once and are relatively young compared to old-growth stands. We quantified foraging behavior, year-round home range, and woodpecker productivity for groups within and proximal to an old-growth longleaf pine (*Pinus palustris*) stand from late 1992 to late 1993 in southwestern Georgia. Average year-round home range size for seven woodpecker groups in and adjacent to the old-growth stand based on minimum 95% convex polygons was 47.1 ha. Year-round home range was negatively correlated with the percentage of the home-range located within old-growth forest. In the old-growth stand the size class distribution of trees selected by woodpeckers for foraging was different than the distribution of trees available in size classes >30 cm dbh. As in other studies, males and females differed in foraging height and parts of the trees used. Clutch size and fledging rates of the seven study groups were also higher than reported in other studies. Red-cockaded Woodpeckers preferentially forage on large (and presumably old) trees. The small year-round home range, high density, large group size, and high productivity indicate that this old-growth longleaf forest is high quality habitat. We suggest that forest management intended to provide an adequate number of replacement cavity trees and quality foraging habitat for the Red-cockaded Woodpecker should have old trees across the landscape. *Received 14 May 1996, accepted 15 Jan. 1997.*

Longleaf pine (*Pinus palustris*) forest dominated an estimated 27 million ha (Wahlenberg 1946) of the southeastern coastal plain before extensive logging in the early 1900s. Today, approximately 5% of the original longleaf pine ecosystem remains in such forests, although most of this is second- or third-growth (Kelly and Bechtold 1990, Outcalt and Outcalt 1994). Based on preliminary estimates, only 3900 ha of old-growth longleaf forest remains (Means 1996). Much of the younger forest lacks important characteristics of old-growth longleaf, such as old trees, vertical and horizontal heterogeneity, and persistent snags (Engstrom, pers. obs.). The importance of the structure and composition of old-growth to organisms that presumably evolved in longleaf pine forests is largely unexplored. This paper documents some of the life history characteristics of one bird species of the longleaf pine ecosystem, the Red-cockaded Woodpecker (*Picoides borealis*).

Habitat requirements of the Red-cockaded Woodpecker have become centrally important to forest management planning for public lands such

[1] Tall Timbers Research Station, Rt. 1, Box 678, Tallahassee, Florida 32312-9712.

as National Forests and military installations in the southeastern United States (Lennartz 1985, McWhite 1993, Meier 1993). Basic needs of the woodpecker include large areas of pine forest for foraging (Henry 1989), trees an average of 90–130 years old or older for cavities (Rudolph and Conner 1991), and contiguity of habitat to facilitate successful dispersal of individuals among groups (Anonymous 1990). Ecosystem management planning for National Forests in the Southeast has focused on providing these habitat features (Meier 1993). Old-growth forest plays an important role in the development of ecosystem management because it serves as a model for understanding natural disturbance and regeneration cycles (Thomas et al. 1988, Sharitz et al. 1992). Additionally, study of the behavior of organisms in old-growth may be instructive because the full suite of forest structural characteristics is available. Most of the research that has been conducted on the Red-cockaded Woodpecker to establish habitat preferences has occurred on forests that have been managed for timber production for decades. Study of woodpecker behavior in old-growth provides information for deciding which old-growth characteristics are important and should be maintained or mimicked in forests for woodpecker management (Lennartz and Lancia 1989).

Our objectives for this study were to measure, for seven Red-cockaded Woodpecker groups, year-round home range and foraging behavior in relation to habitat structure and composition in or near an old-growth longleaf pine forest. We also measured group size, clutch size, and fledging rate for the study groups.

METHODS

The Wade Tract is an 80-ha old-growth longleaf pine forest preserve in southwestern Georgia (30°46′30″N, 84°00′W) that has been preserved in a long-term conservation easement since 1979. The easement is privately owned, but it is managed by Tall Timbers Research Station for research purposes. For a study of forest structure and dynamics the easement was gridded with permanent metal stakes at 100-m intervals, all trees ≥1.5 m in height were given numbered aluminum tags, and tree locations were surveyed on 39.4 ha of the easement (Platt et al. 1988).

The forest is characterized by a negative exponential size class distribution and considerable patchiness (Platt et al. 1988, Engstrom and James 1981). Tree species composition of the canopy is >90% longleaf pine with scattered hardwoods and other pine species. Hurricanes, fires, and small gaps caused by death of an individual or small groups of trees are disturbances that shape the forest. As far as known, only individual trees that were killed by lightning or insects were harvested for salvage before the area was made into an easement. Canopy trees are 200–400 years old (Platt et al. 1988, Engstrom, pers. obs.).

Currently, each half of the Wade Tract (the plot is roughly bisected by a dirt road that runs from cluster 3 to cluster 2 in Fig. 1) is burned biannually in the lightning season (May–June) on an alternating schedule. Previous to the establishment of the conservation easement, the entire preserve was burned annually during the dormant season (usually early March). The preserve is bounded to the east by a 30-m wide paved road and grassy shoulder with

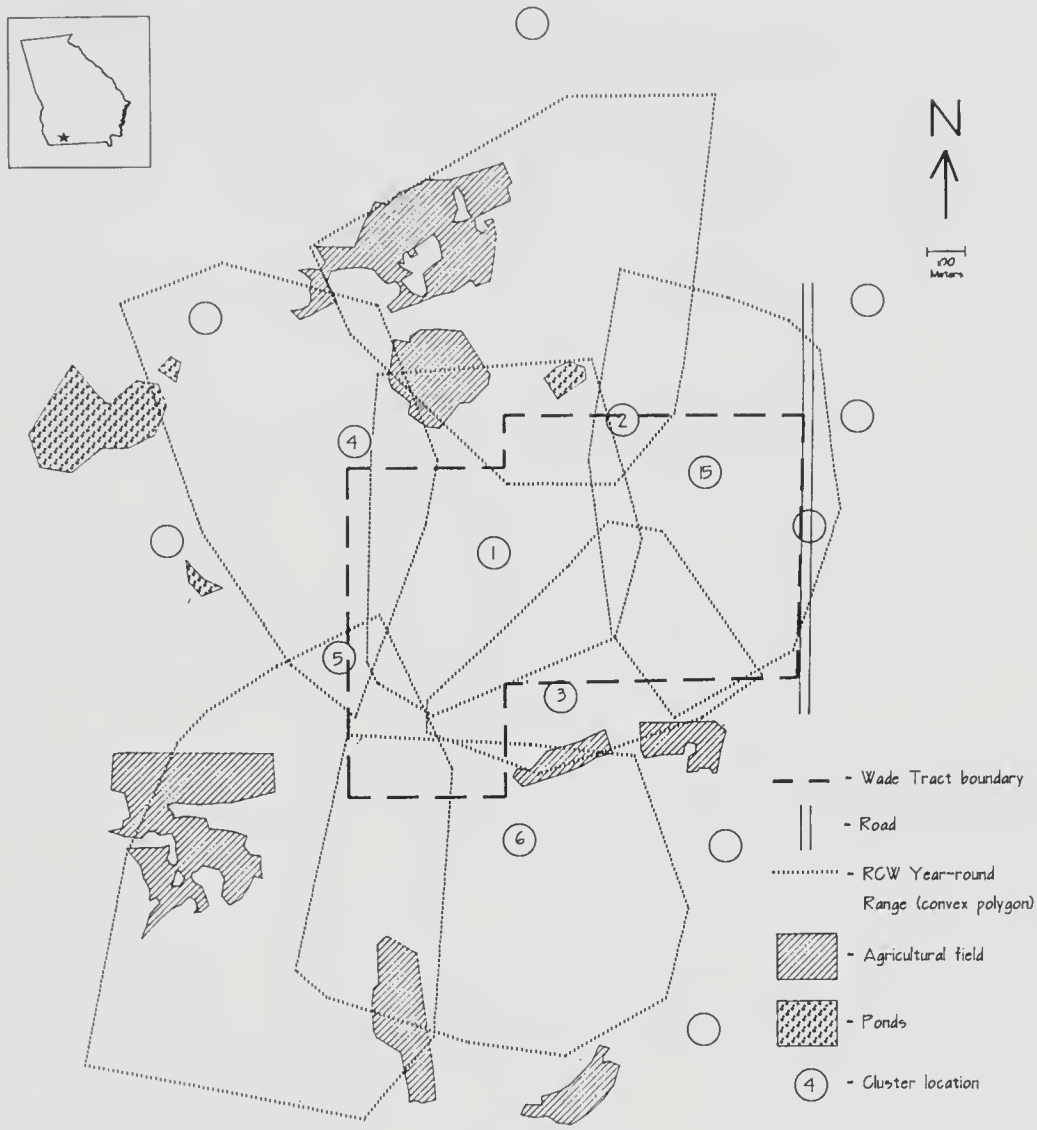

FIG. 1. Year-round home ranges of seven Red-cockaded Woodpecker study groups in old-growth longleaf pine forest indicated as convex polygons. The numbers within circles identify the study groups and the eight empty circles represent active clusters surrounding the study clusters.

similar old-growth habitat to the east of the road. Longleaf pine forest that is managed with single-tree selection silviculture is the habitat on all sides of the preserve. Fields and ponds are interspersed within this area (Fig. 1).

Some or all of the cavity trees of eight clusters are on the preserve. Seven of the groups that lived in these clusters were included in this study. The eighth group lived primarily on adjacent property (unnumbered circle that straddles the paved road in Fig. 1) and was not included in the study. Seven additional active clusters surround the preserve in the managed forest. Outside the preserve, old trees are retained within the clusters and scattered throughout the forest that is managed for quail hunting, aesthetics, timber production, and conservation of native flora and fauna (Engstrom and Baker 1995). Woodpecker cavity trees and potential cavity trees are retained within clusters in local timber management practices. The

timber management approach includes selective tree harvest on an approximately 10-year cutting cycle in the managed forest (Neel 1971, Lindeman 1994). All clusters in this regional population (179 active clusters) are located on privately owned land (Engstrom and Baker 1995).

Each of the seven study groups was followed for as long as possible on at least one day in almost every month for a total of 476 h from December 1992 through December 1993. The number of hours per group for the entire year ranged from 57 to 78, and the average number of hours followed per group per month ranged from 4.8 to 6.0. Three groups (1, 2, and 6) were not followed during May, and Group 5 was not followed during March and April.

We plotted locations of the groups on 1:7200 scale aerial photographs, transferred them to base maps, and eventually digitized them into Generic CADD 6 (Anonymous 1993). Significant features of the landscape, such as agricultural fields, ponds, roads, and the preserve boundary, also were digitized and entered into Generic CADD 6. We determined areas of convex polygons of year-round home ranges and suitable and unsuitable habitat with Generic CADD 6. We calculated minimum convex polygons (95%) for each year-round home range (Program Home Range, Ackerman et al. 1990). A Pearson product moment correlation coefficient was calculated between the 95% convex polygon of each year-round home range and the percent of the home range in the Wade Tract (Zar 1984, Minitab 1991).

Linear distances from the center of cavity tree clusters (estimated visually) to foraging locations were measured on the base maps to determine the extent of movements in relation to time of day. LOWESS (Locally Weighted Scatterplot Smoothing) was used to display graphically the relationship between time of day and distance from cluster (SYSTAT Version 5.03: Wilkinson 1990a).

We took single-point observations of foraging behavior of individuals in the seven study groups using a 25× spotting scope. Single-point observations were used to avoid inter-observation dependence (Hejl et al. 1990). One foraging behavior was noted per individual on a given tree immediately after the identity of the individual was established. Foraging behavior categories, excavating (making a hole by removing wood), probing (using the bill to search beneath the surface of the bark), gleaning (search in foliage), scaling (removal of flakes of bark), and moving and looking, are described in Hooper and Lennartz (1981). After we recorded identity of each individual and foraging behavior, we noted tree diameter at breast height (dbh), height of the woodpecker on the tree, tree height, substrate used (trunk, live branch, dead branch, and cone), and position on the tree. To categorize position, the tree was divided into crown (area with the majority of limbs) and upper, middle, and lower thirds of the trunk (below the crown, but sometimes with a few limbs). Height of the woodpecker on the tree and tree height were measured with a clinometer. If the tree being used by a woodpecker was located within the part of the conservation easement in which all trees were tagged, the tree number was recorded.

After the year-round home ranges were determined, the area that comprised the home ranges was divided into stands of similar structure and composition as determined by visual evaluation. A grid was laid over the photo of each stand, and at least six points were randomly selected within each stand. Circular samples (0.04-ha) were taken at each point (James and Shugart 1970). Diameters of all trees ≥4 cm were measured and species identity determined within each circle.

Almost all adult and nestling woodpeckers in the seven woodpecker groups in the study area were banded with U.S. Fish and Wildlife Service aluminum bands and plastic color bands. Group size was established during the nesting season.

Cavity trees in the study clusters were monitored from early April in 1993 and 1994 to establish (1) the nest tree, (2) nesting initiation, (3) clutch size, (4) number of nestlings

TABLE 1

RED-COCKADED WOODPECKER YEAR-ROUND HOME RANGE IN AND AROUND THE WADE TRACT

Group	Year-round home range (ha)	Area of suitable habitat	Percentage in Wade Tract	95% convex polygon
1	55.4	52.3	83	42.6
2	74.5	60.4	11	55.4
3	33.9	32.4	76	23.2
4	60.3	59.0	15	45.4
5	91.3	78.5	11	61.9
6	69.5	66.3	10	56.8
15	58.3	55.9	63	44.6
Mean	63.3	57.8		47.1

when the nestlings were approximately 8 days old, and (5) the number of fledglings within 30 days after the departure from the nest.

RESULTS

The areas of 95% minimum convex polygons of the year-round home ranges of the seven Red-cockaded Woodpecker groups in and proximal to the old-growth longleaf pine forest ranged from 23.2 to 61.9 ha, with a mean of 47.1 ha (Table 1). The percentage of the home range within the Wade Tract had a significant negative Pearson product moment correlation coefficient ($r = -0.781$) with home range area. Using total year-round home range for comparability, the Wade Tract areas were smaller than those reported for other studies, except for Wood (1983), who measured home range for only one group (Table 2). When unsuitable habitat, such as agricultural fields, ponds, and roads were excluded, the mean amount of suitable habitat within the home range for the seven study

TABLE 2

TOTAL YEAR-ROUND HOME RANGE AREAS (HA) FROM OTHER STUDIES IN COMPARISON WITH THIS STUDY

Citation	Location	Mean (N)	Range
Wood (1983)	OK	53 (1)	—
Hooper et al. (1982)	SC	87 (24)	34–225
Porter and Labisky (1986)	FL	129 (4)	85–157
DeLotelle et al. (1987)	FL	150 (6)	116–199
Jackson and Parris (1995)	LA	pre-clearing 135 (3)	109–170
		post-clearing 253	115–413
This study	GA	63 (7)	34–91

groups was 57.8 ha. One complication was that some of the agricultural fields, which were included as unsuitable habitat, were corn fields. Red-cockaded Woodpeckers have been noted to eat corn ear worms and other arthropods on corn in the past (Baker 1971), and groups were seen to forage on corn in this study. Thus, corn fields provided an ephemeral food supply during the critical fledgling period, but the fields were unusable for most of the year.

Considerable overlap occurred in the home ranges. For example, 31% of the 52.3 ha home range of Group 1 overlapped with other groups (Fig. 1). Estimating the percentage of overlap of the other study groups was not possible, because each of these groups have additional neighboring groups whose home ranges were not measured. Observations of one group of woodpeckers entering the cluster area of another group were made on several occasions. Territorial interactions, such as wing displays, calling, and looping flights (Ligon 1970) were observed when two groups came into contact, but the intensity of the displays varied considerably. Occasionally, two groups that were foraging in the same area mingled with very little display.

The groups tended to move the maximum distance from the cluster by five hours after sunrise (determined by visual estimate of the asymptote of the LOWESS line in Fig. 2); however, this relationship varied considerably. For example, by the seventh hour after sunrise, distance from the cluster ranged from 0.1 to 1.1 km.

A total of 1380 observations of foraging behavior of individuals in the seven study groups were collected simultaneously with the year-round home range data from December 1992 through December 1993. The number of observations per group ranged from 150 to 242. Excavations and probes made up 69 percent of all foraging behaviors recorded. Scaling (15%), hitching and looking (10%), other (5%), and gleaning (2%) made up the rest of the observations. The frequency of gleaning may have been underestimated because of the difficulty of observing this behavior in clumps of needles high in the trees. Both excavations and probes have a strong seasonal component (Fig. 3), with excavations more common in the spring and summer than in the fall and winter. A few observations were made of woodpeckers feeding on ears of corn, but the groups were not followed closely in the corn fields.

As in other studies of Red-cockaded Woodpecker foraging behavior, males tended to forage higher in trees than females (mean height: males = 16.4 m, N = 945; females = 15.1 m, N = 404; $P \leq 0.001$, Mann-Whitney U-test). This was also reflected in the position on the tree (Table 3) and the substrate used by the sexes (Table 4). Males tended to forage in the crown more than females, and females spent more time than males

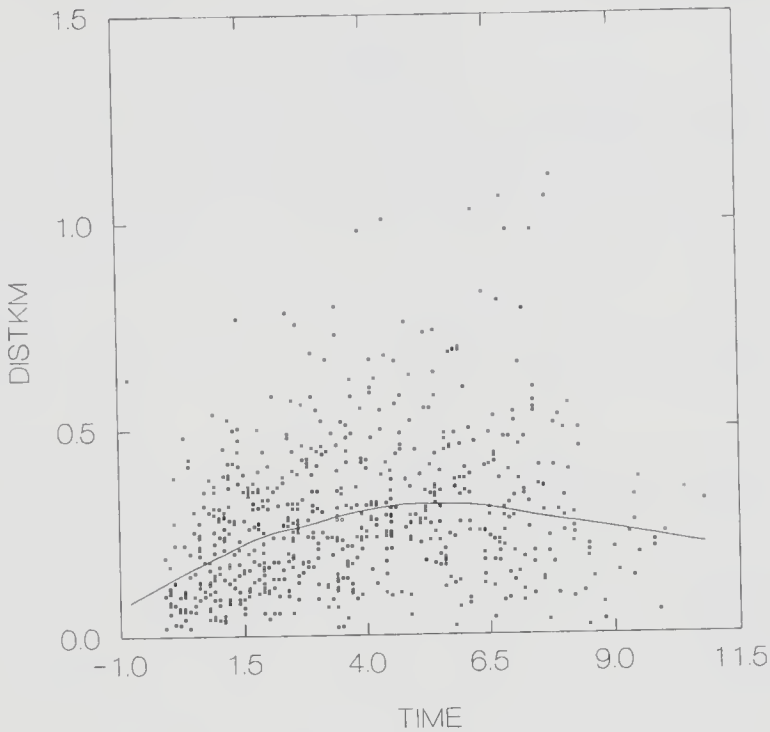

FIG. 2. Distances (km) that Red-cockaded Woodpecker study groups moved from the home cluster as a function of the number of hours since sunrise. The line through the points is a LOWESS plot.

on the lower and middle parts of the trunk. Males also made 35% more foraging visits to branches, living and dead, than did females. The area included within all seven woodpecker year-round home ranges was divided into nine stands based on forest structure and composition. Between

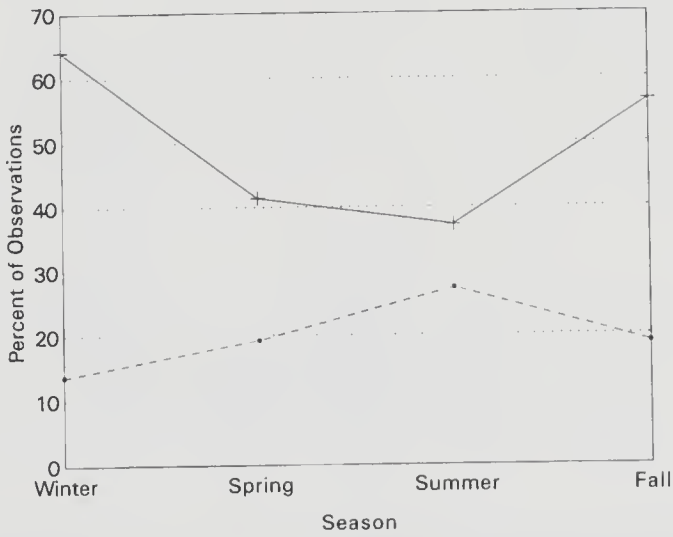

FIG. 3. Seasonal variation in the frequency of foraging behaviors.

TABLE 3

DIFFERENCES BETWEEN THE SEXES IN THE PERCENTAGE OF THE NUMBER OF OBSERVATIONS OF FORAGING BEHAVIOR FOR DIFFERENT POSITIONS ON A TREE

	CR	LOW	MID	UPP	OTH	TOTAL	N
F	65.13	12.35	9.20	12.11	1.21	100.00	413
M	79.32	2.69	5.27	11.27	1.45	100.00	967
N	1036	77	89	159	19	—	1380

[a] CR = crown; LOW, MID, UPP = thirds of trunk.

six and 38 0.04-ha circular samples were taken in the stands for a total of 129 samples. When all stands were combined within a year-round home range, the estimated numbers of pines (all species) ≥25.4 cm dbh ranged from 2341 to 5729 per group ($\bar{x}$ = 4504, SD = 1169, Table 5).

Based on 38 0.04-ha vegetation samples within the old-growth stand (39.4 ha plot), the size class distribution of trees was approximately an inverse J shape. Stems were most common in the 1–10 and 10–20 cm dbh size classes, underrepresented in the 20–40 cm dbh classes, and about as expected in the >40 cm dbh classes (Fig. 4).

Nearly 80% of the trees selected for foraging by Red-cockaded Woodpeckers in the old-growth forest were between 35 and 65 cm dbh. Using tree distribution and woodpecker foraging data from the old-growth stand only (nine 10-cm size classes: 1–10, . . . 81–90), a Chi-square test of the null hypothesis that the woodpeckers were selecting trees in relation to their availability can be rejected (χ^2 = 351, df = 8, $P < 0.001$). The number of trees used in the smallest size classes (1–10, 11–20 cm dbh) were used less than the 95% confidence intervals for the number of trees available in those classes, and trees in size classes from 31 cm dbh and higher were used in excess of the 95% confidence intervals for those classes (Wilkinson 1990b). When the two smallest size classes were deleted and the top two intervals combined, the null hypothesis was still

TABLE 4

DIFFERENCES BETWEEN THE SEXES IN THE PERCENTAGE OF THE NUMBER OF OBSERVATIONS OF FORAGING BEHAVIOR FOR DIFFERENT PARTS OF A TREE

	BR	CON	DBR	OTHER	ROOTS	TR	TOTAL	N
F	16.95	3.15	3.63	0.73	0.24	75.30	100.00	413
M	32.16	3.72	23.16	0.93	0.00	40.02	100.00	967
N	381	49	239	12	1	698		1380

[a] BR = branch; CON = cone; DBR = dead branch; TR = trunk; ROOTS = upturned roots.

TABLE 5

SUMMARY OF THE NUMBER OF TREES IN EACH YEAR-ROUND HOME RANGE[a]

	Longleaf		Other pine		Hardwoods		Hardwood snag		Pine snag	
Group	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
1	4424	3742	41	93	1137	8	466	6	69	142
2	2377	5314	26	352	1510	83	1687	0	9	22
3	3483	2315	0	26	703	57	201	0	133	83
4	2993	4347	288	614	1436	33	322	74	173	64
5	11,407	4467	5907	1262	4540	712	656	0	365	136
6	10,566	4287	828	281	205	1080	142	0	172	115
15	3924	4323	77	101	1266	33	926	0	59	115

[a] Large = ≥25.4 cm and small = ≥2, and <25.4 cm.

rejected ($\chi^2 = 20.16$, df = 5, $P < 0.005$). Trees used exceeded the 95% confidence interval of trees available in the 61–70 cm dbh size class in this reduced data set.

Group sizes of the seven study groups ranged from two to five individuals when nestlings were being fed (Table 6). In 1994 groups were larger, nested earlier, had a higher clutch size, more nestlings, but fewer fledglings. In both years one of the seven groups failed to produce any fledglings.

DISCUSSION

Year-round home ranges of the seven Red-cockaded Woodpecker groups in and around the Wade Tract were smaller than home ranges

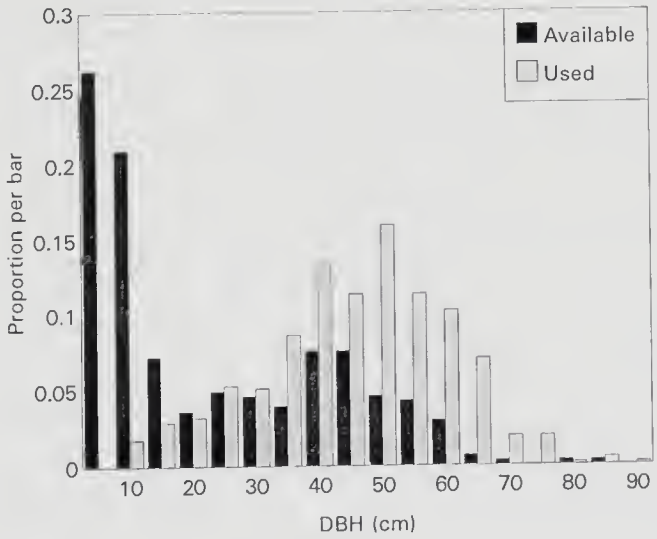

FIG. 4. Size class distribution of trees in the Wade Tract compared to the size class distribution of trees used by Red-cockaded Woodpeckers for foraging.

TABLE 6
SIZE AND PRODUCTIVITY OF SEVEN RED-COCKADED WOODPECKER GROUPS IN AND AROUND THE WADE TRACT

	1993	1994
Mean number of adults	3.0	3.6
Mean date of first egg	25 April	19 April
Mean clutch size	3.3	3.6
Mean number of nestlings	2.5	2.5
Mean number of fledglings	2.5	2.3
Percent of failed nests	14	14

measured in most other studies (Table 2). R. Hooper (in Lennartz 1985) reported 22 clans in an approximately 1000-ha expanse of mature heavily stocked longleaf pine forest. This equaled an estimated density of one group in 45 ha, but this may underestimate year-round home range because of overlap. We found that home ranges overlapped widely. Over 30 percent of the home range of Group 1, which held the most central position within the Wade Tract (Fig. 1), was shared by other groups. Amount of overlap for the peripheral study groups could not be determined because groups beyond the periphery were not followed. We did not determine defended territory size as a subset of home range.

Although the Red-cockaded Woodpecker is described as having a Type A territory (Ligon 1970), we and other authors (Hooper et al. 1982, DeLotelle et al. 1987), have noted movements by groups into the home range and even the cavity tree clusters of neighboring groups. DeLotelle et al. (1987) determined territory sizes of Red-cockaded Woodpeckers in central Florida based on locations of territorial encounters, but observed the same number of extraterritorial movements as territorial defenses. Porous home range boundaries are probably a function of the difficulty of defending such large foraging areas.

Determination of home range size is partly a function of how many hours a group is followed by observers during the day (e.g., Nesbitt et al. 1978). Some of the longest distances that groups moved away from the center of the home cluster were late in the day (Fig. 2). These long distance movements, although relatively rare, can strongly affect overall home range size. Usually, however, the maximum distance the groups traveled during a day tended to be within the first five hours. Using a different approach, Hooper and Harlow (1986) also found that woodpeckers followed for five hours provided unbiased estimates of territory size when compared to whole-day samples. Given the difficulty in ob-

taining whole-day samples, we recommend five-hour sampling periods for estimating home range size.

Inter-sexual foraging behavior of the woodpecker in old-growth forest was similar to behavior described in other studies. Males foraged higher in the trees, more in the crown (Table 3), and used more branches (Table 4) than females. This is consistent with the results of Ligon (1968) and Hooper and Lennartz (1981). We also found a strong seasonal component to foraging: excavations tended to be more frequent in the spring and summer and probes more frequent in the fall and winter (Fig. 3). This is somewhat consistent with the observations of Hooper and Lennartz (1981), but they divided the year into three sections; therefore, the results are not directly comparable to ours. Conner (1981), however, described different seasonal patterns of foraging for Downy (*Picoides pubescens*), Hairy (*P. villosus*), and Pileated (*Dryocopus pileatus*) woodpeckers. In all three species, excavations were more common in the winter than in the breeding or post-breeding seasons, and "peer-and-poke," which is similar to our "probe," was more common in the breeding and post-breeding seasons than in the winter. Higher use of limbs by females in this study (20.6%) compared to 4.3% in Hooper and Lennartz (1981) may be a function of larger crowns in the old trees at the Wade Tract.

Although the Wade Tract study groups are few in number and not randomly sampled, it is noteworthy that average group size tended to be three or larger in the two years of study (Table 6). Also, no single males were found defending clusters in the Wade Tract. The presence of helpers may be partially a function of habitat saturation (Walters 1990). The Wade Tract study groups have 32 active groups within 3.2 km (median dispersal distance of first year females, Walters et al. 1988), which is a very high population density (Engstrom and Mikusinski, unpub. data).

Productivity of fledglings (2.3–2.5 per nest per year, exclusive of failed nests) at the Wade Tract is also relatively high. LaBranche and Walters (1994) reported a mean number of young fledged per successful nest of 1.9 in 929 nests monitored from 1980 to 1985 in North Carolina. DeLotelle et al. (1995) reported mean fledging rates of 0.4–1.4 (grand mean = 1.0) and mean group size of 2.3 for a 12-year study in central Florida. High productivity in a region of high density indicates that density is not a misleading indicator of habitat quality (Van Horne 1983).

The Red-cockaded Woodpecker has declined precipitously in response to land use changes in the southeastern coastal plain in the twentieth century. Recovery of this species should be grounded in an ecosystem management approach that mimics natural forms of disturbance (e.g., Sharitz et al. 1992). In theory, this approach will provide habitat for plants and animals that are most adapted to the ecosystem, even species that are

not and probably never will be studied, as well as the Red-cockaded Woodpecker.

Probably more than any other bird species, the Red-cockaded Woodpecker depends on some old-growth characteristics of southeastern pine forests. Although extensive old-growth pine forests have been eliminated from the southeastern landscape, scattered remnant trees and patches of old-growth likely provided a crucial bridge for the Red-cockaded Woodpecker into a second-growth forest. Red-cockaded Woodpecker life history requirements are pivotal considerations in National Forest and other public land management in the southeastern United States (Lennartz et al. 1983, Meier 1993). Foraging guidelines for the woodpecker have been based largely on research that was conducted in forests that have significantly modified tree species composition, age structure, and landscape arrangement. Public land managers must address what old-growth characteristics should be retained within managed forest and in what spatial arrangement (Lennartz and Lancia 1989).

High local population density, high productivity, and small year-round home range size indicate that the Wade Tract old-growth longleaf pine forest is excellent habitat for the Red-cockaded Woodpecker. The exact contribution of foraging habitat quality to productivity is not clear. For example, the abundance and quality of cavity trees also may have played a role. Although the Wade Tract may be an unusually productive forest, Red-cockaded Woodpeckers in this study, as in other studies, tended to forage on the largest (and probably oldest) trees in the forest (e.g., DeLotelle et al. 1983). At the stand level, Hooper and Harlow (1986), however, found no evidence that the occurrence of large pines affected stand selection for foraging. They also concluded that pines 24 to 35.6 cm dbh appear to be as valuable as trees ≥36 cm dbh for foraging. Our results indicate that large and old trees are used preferentially.

We disagree with the conclusion by Hooper and Harlow (1986) that "thinnings, superior stock, fertilization, initial spacing at regeneration, and site index may be as important as age in providing quality foraging habitat." These silvicultural techniques may provide larger trees faster at the expense of trees that are of high value to wildlife, especially the Red-cockaded Woodpecker. Old, co-dominant or suppressed trees may have microhabitats, such as dead limbs, that are important to ants and other arthropods. We recommend that management for Red-cockaded Woodpeckers include retaining old trees throughout the landscape, not just in the cluster to serve as replacement cavity trees.

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CONSUMPTION OF COLORED AND FLAVORED FOOD MORSELS BY HARRIS' AND AMERICAN TREE SPARROWS

ROBERT J. ROBEL,[1,4] JEFFREY F. KEATING,[1] JOHN L. ZIMMERMAN,[1] KEITH C. BEHNKE,[2] AND KENNETH E. KEMP[3]

ABSTRACT.—Extruder-produced food morsels of different colors and flavors were offered to Harris' Sparrows (*Zonotrichia querula*) and American Tree Sparrows (*Spizella arborea*). The consumption of these morsels was measured to determine positive or negative selection by these two species of birds. Birds consumed more brown and yellow morsels than blue or orange morsels and more butter-/and nut-flavored morsels than lime-flavored morsels. In this study, color selection probably reflected avoidance of blue and orange morsels, rather than a preference for brown and yellow morsels. Color discrimination among our birds was stronger than flavor discrimination. Elucidation of color and flavor preferences and avoidance characteristics may prove useful in developing granular pesticide delivery systems that reduce potential hazards for birds. *Received 21 June 1996, accepted 15 Jan. 1997.*

Animals use various cues to locate and select food items. Eyes enable animals to discern size, shape, and color of potential food items, whereas taste buds allow them to discriminate among food items by flavor. The large size of birds' eyes, up to 1.5% of total body mass (Welty 1982), reflects the importance of the sense of vision to birds. The structure of the avian eye resembles that of other vertebrate eyes, and visual pigments in cone cells of birds convey color vision (Govardovskii and Zueva 1977). Selection and avoidance of certain colored food items by several avian species confirm that birds can discern among colors (Pank 1976, Slaby and Slaby 1977).

The existence of flavor perception in birds is supported by the presence of taste receptors (Duncan 1960) and by preference testing experiments. Positive and negative responses by birds to sweet, bitter, acid, and salt solutions reflect their ability to taste (Warren and Vince 1963, Brindley 1965, Grieg-Smith 1985). Reduction in the consumption by birds of food contaminated by toxic materials is further evidence for flavor perception in avian species (Bennett and Prince 1981; Robel et al. 1982, 1985).

Both flavor and color discrimination have become important in developing delivery systems for aversion learning techniques to reduce depredation damage caused by birds (Mason and Reidinger 1983a, b; Mason

[1] Div. of Biology, Kansas State Univ., Manhattan, Kansas 66506-4901.
[2] Dept. of Grain Science and Industry, Kansas State Univ., Manhattan, Kansas 66506-2201.
[3] Dept. of Statistics, Kansas State Univ., Manhattan, Kansas 66506-0801.
[4] To whom correspondence should be sent.

TABLE 1

DYE SOLUTION ADDED TO BASE MIX TO PRODUCE COLORED FOOD MORSELS

Dye dissolved in 300 ml H_2O		Color of food morsel[a]	Termed in text
25 g Warner-Jenkinson[b]	05601 FDC-blue No. 1	Black10Cyan-blue70Yellow 40	Blue
25 g Stange[c]	CO1355 Chocolate	Black40Yellow50Magenta-red30	Brown
25 g Warner-Jenkinson	08005 FDC-yellow No. 5	Yellow60Magenta-red20Cyan-blue10	Yellow
8 g Warner-Jenkinson plus 17 g Warner-Jenkinson	07700 FDC-red No. 40 / 08006 FDC-yellow No. 6	Yellow50Magenta-red50Cyan-blue10	Orange

[a] Color compared to Color Atlas plates (Keuppers 1982).
[b] Source: Warner-Jenkinson, Inc., St. Louis, Missouri 63106.
[c] Source: Stange Co., Chicago, Illinois 60612.

et al. 1989). Little research has been conducted to increase acceptability of bird feeds by altering their color or incorporating a flavor additive. This study was conducted to determine the effect of different colors and flavor additives on consumption of extruder-produced food morsels by Harris' Sparrows (*Zonotrichia querula*) and American Tree Sparrows (*Spizella arborea*).

METHODS

Food morsels were formulated and processed through an extrusion cooker (Wenger X-20 LBM). The food morsels were composed of yellow corn (66%, dry weight), grain sorghum (16%), hard red wheat (6%), soybean meal (5%), and soybean oil (3%) plus minerals and vitamins. Extruder-produced food morsels were used because they could be made uniform in energy content, shape, size, firmness, and surface texture. (Keating 1989, Keating et al. 1990)

The spherical food morsels measured 1.59 mm in diameter, and their natural color was tan [Black10Yellow40Magenta-red10 (Keuppers 1982)], closely resembling seeds of white proso millet (*Panicum miliaceum*). Food morsels were colored by adding a solution of organic food dye to the base mix in the extruder. Dyes used, dilution factors, and colors of food morsels produced are shown in Table 1. After morsels were dried, they were placed in paper feed bags and stored in dry conditions at room temperature until used.

An excess of yellow-colored morsels was produced for use in flavor preference studies. These morsels were coated with liquid fruit, butter, or nut flavors. Fries and Fries brand liquid flavors were used; artificial lime (flavor No. 139121) for fruit, artificial butter (flavor No. 153979) for butter, and equal portions of artificial pecan (flavor No. 153972) and artificial nut (flavor No. 153973) for nut. The undiluted lime flavoring constituted 0.75% by weight of the finished feed, whereas the undiluted nut and butter flavorings constituted 1.0 to 2.0% by weight of the finished feed. Flavored morsels were placed into air-tight containers and stored in darkness until used.

Harris' Sparrows and American Tree Sparrows were captured in mist nests (Federal Permit No. PRT-689136) and confined individually in 39 × 22 × 27-cm wire cages inside a walk-in environmental chamber maintained at 5°C and 75% relative humidity under a 10-h light:

14-h dark photoperiod. Birds were captured in late November and acclimated to chamber conditions for at least 10 days before any feeding preference data were gathered. Birds were provided white proso millet, sunflower (*Helianthus* spp.), and a mixture of grass seeds when first confined and gradually weaned to a diet of only chick starter mash (ingredients and composition in Keating [1989]) by the end of their 10-day acclimatization period. All test morsels were included in the rations eight days prior to initiation of feeding trials to reduce unfamiliarity/novelty biases. Water and food were provided *ad libitum*.

Separate feeding trials were conducted to determine if the birds preferentially selected food morsels by color or flavor. Color preference trials preceded flavor preference trials. One replicate of a 6 × 6 Latin Square experimental design, incorporating 12 birds of each species, was used in color feeding trials; birds (6) and days (6) were the blocking factors. One replicate of a 3 × 3 Latin Square design, using six birds of each species, was used for flavor feeding trials; birds (3) and days (3) were the blocking factors. The Harris' Sparrows had a mean body mass of 35.7 g (range 31.6 to 39.4 g), whereas the mean body mass of American Tree Sparrows was 18.4 g (range 15.6 to 20.8 g).

Feeding trials consisted of pair-wise presentations of all combinations of colored or flavored morsels for two consecutive days to each of the 24 birds. At the onset of the daily light period, pre-weighed amounts of paired morsels (singly and in excess of expected daily consumption) were placed in clear plastic feeders at opposite ends of each bird's confinement cage. Four times each day, all feeders were refilled so that no feeder ever became half-depleted. Feeder positions were exchanged when they were refilled to avoid position bias. Food remaining in each feeder and spilled food was removed at the end of the light period, and the total mass of each morsel type consumed during the day was determined. Bird preferences for morsels of different colors or flavors were determined by subjecting consumption data (mass) to analysis of variance (ANOVA) procedures (Kemp et al. 1990) with significance at $P = 0.05$. The above methodology was also used to compare the consumption of naturally colored and naturally flavored food morsels to that of the most preferred artificially colored and artificially flavored morsels.

RESULTS

When brown-colored morsels were paired with yellow morsels in feeding trials, no differences in the consumption of the two occurred (Table 2). However, when brown- or yellow-colored morsels were paired with blue- or orange-colored morsels, greater masses of yellow and brown morsels were consumed. Total consumption by the larger Harris' Sparrows exceeded that of the smaller American Tree Sparrows by approximately 50%. No birds died and mean body masses of experimental birds did not change by more than ±5% during any of the feeding trials. Consumption of colored and flavored food morsels on the first and second day of a test replication did not differ (ANOVA, $P < 0.05$), indicating no learning by the birds during the feeding trials.

Harris' Sparrows ate significantly (ANOVA, $P < 0.05$) more brown and yellow morsels than orange morsels (Table 3). Blue morsels were consumed significantly (ANOVA, $P < 0.05$) less than brown, yellow, or orange morsels by Harris' Sparrows. American Tree Sparrows consumed similar amounts (ANOVA, $P > 0.05$) of brown and yellow morsels, but

TABLE 2

MEAN (±SE) MASS (G) OF COLORED AND FLAVORED FOOD MORSELS CONSUMED DURING PAIR-WISE PRESENTATIONS

Pair-wise presentations	Mean[a] daily consumption	
	Harris' Sparrow	American Tree Sparrow
Colored morsels		
Brown	6.15 ± 0.30	3.96 ± 0.29
Blue	3.44 ± 0.33	2.12 ± 0.30
Blue	4.17 ± 0.39	2.73 ± 0.42
Orange	5.23 ± 0.38	3.28 ± 0.40
Yellow	6.29 ± 0.31	4.05 ± 0.37
Blue	3.18 ± 0.33	2.10 ± 0.40
Brown	5.60 ± 0.29	4.01 ± 0.21
Orange	3.83 ± 0.35	2.12 ± 0.20
Brown	4.88 ± 0.24	2.86 ± 0.30
Yellow	4.45 ± 0.30	3.17 ± 0.26
Yellow	5.58 ± 0.32	4.17 ± 0.25
Orange	3.87 ± 0.30	1.99 ± 0.29
Flavored morsels		
Butter	5.12 ± 0.42	3.94 ± 0.38
Lime	4.16 ± 0.33	2.33 ± 0.23
Butter	4.95 ± 0.37	3.30 ± 0.29
Nut	4.59 ± 0.39	3.05 ± 0.22
Nut	5.07 ± 0.38	3.92 ± 0.25
Lime	4.37 ± 0.30	2.20 ± 0.28

[a] Means of 2 daily measurements for 12 birds, N = 24.

significantly (ANOVA, $P < 0.05$) more than amounts of orange and blue morsels, whose consumptions also did not differ significantly (ANOVA, $P > 0.05$) from each other (Table 3).

The daily consumptions of brown (5.00 ± 0.27 g) and yellow (4.25 ± 0.27 g) morsels by Harris' Sparrows were not significantly (ANOVA, $P > 0.05$) different than the 4.24 ± 0.27 g consumption of uncolored morsels. However, the daily consumptions of brown (3.34 ± 0.33) g and yellow (3.10 ± 0.33 g) morsels by American Tree Sparrows were significantly (ANOVA, $P < 0.05$) greater than the 2.00 ± 0.33 g consumption of uncolored morsels.

When butter-flavored morsels were paired with nut-flavored morsels in feeding trials, no differences in the consumption of the two occurred (Table 2). However, when lime-flavored morsels were paired with butter-

TABLE 3
RANKED MEAN MASSES (G) OF COLORED AND FLAVORED MORSELS CONSUMED DAILY DURING FEEDING TRIALS

Morsels	Harris' Sparrows	American Tree Sparrows
Colored		
Brown	5.56a[a]	3.60a
Yellow	5.44a	3.81a
Orange	4.34b	2.46b
Blue	3.59c	2.33b
Flavored		
Butter	5.03a	3.62a
Nut	4.83a	3.46a
Lime	4.26b	2.26b

[a] Means (N = 72 for color, 48 for flavor) within a column in the same morsel category sharing a common letter do not differ (ANOVA, $P > 0.05$).

or nut-flavored morsels, the consumption of these latter morsels tended to increase. The total consumption of flavored morsels by the larger Harris' Sparrows was approximately 50% greater than that by the smaller American Tree Sparrows.

The amounts of butter-flavored morsels consumed by Harris' Sparrows were not significantly (ANOVA, $P > 0.05$) different than the amounts of nut-flavored morsels consumed (Table 3). However, the consumptions of both butter- and nut-flavored morsels by Harris' Sparrows were significantly (ANOVA, $P < 0.05$) greater than that of lime-flavored morsels. The same relationship held for American Tree Sparrows.

Harris' Sparrow's daily consumption of butter-flavored morsels (5.01 ± 0.14 g) was not significantly different (ANOVA, $P > 0.05$) than the 4.73 ± 0.14 consumption of unflavored morsels. Likewise, the daily consumption by American Tree Sparrows of butter-flavored morsels (3.11 ± 0.13 g) was not significantly different (ANOVA, $P > 0.05$) than the 3.17 ± 0.13 g consumption of unflavored morsels.

DISCUSSION

Both Harris' Sparrows and American Tree Sparrows demonstrated the ability to discern color by selecting certain colors of food morsels over others. These results support other studies that reported color perception in birds. The reduced consumption of blue and orange morsels may reflect avoidance of novel food colors rather than a positive selection of brown and yellow colors. Rabinowitch (1968) found that birds selected food items to which they became familiar in early life and avoided novel-

colored items. Blue- and orange-colored seeds are not frequently encountered by wild Harris' Sparrows or American Tree Sparrows in the midwestern United States, whereas brown- and yellow-colored seeds are common. Thus, it appears that rather than selecting brown and yellow morsels, our birds were actively avoiding blue and orange morsels. This agrees with conclusions advanced by Kalmback (1943) and Ridsdale and Granett (1969) that food consumption by birds is deterred by certain colored seeds. Gionfriddo and Best (1996) also reported that color affected avian consumption of differently colored granules. Knowing which colors are avoided by which avian species could be helpful in the development of safer applications of pesticides, but the issue is complex (e.g., see Best and Fischer [1992]).

Our Harris' Sparrows and American Tree Sparrows showed selective tendencies based on flavor, supporting results from studies reported by Westbrook et al. (1980) and Grieg-Smith (1985). However, flavor discrimination was not as strong as color discrimination in the earlier feeding trials, e.g., differences in daily consumption of different flavored morsels were less than among different colored morsels. Flavored morsels used in the study were not consumed in greater amounts than unflavored morsels, further reflecting the weakness of discrimination for these flavors by Harris' and American Tree sparrows. Grieg-Smith (1985) reported that certain polyphenols are distasteful to some birds and, if consumed, interfere with protein digestion. Thus, flavor recognition by birds may assist them to avoid distasteful or harmful food items but may not be a significant positive force to increase consumption of any specific food item. Certain distasteful flavors might be used commercially to reduce consumption by birds of surface-applied granular pesticides.

Additional experimental research, involving more avian species, will provide a clearer understanding of the influences of color and flavor on food choice in birds. That knowledge, in conjunction with such information on morsel shape and size (Keating et al. 1992) and surface texture and shape (Best and Gionfriddo 1994), may be useful in producing (1) granular formulations of pesticides that are less attractive to birds and/or (2) extruded food morsels that are more attractive to birds. Further, such information may also aid the development of effective conditioned avoidance delivery systems to reduce bird damage (Clark and Mason 1993, Avery et al. 1995).

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NATAL DISPERSAL AND PHILOPATRY OF SOUTHEASTERN AMERICAN KESTRELS IN FLORIDA

KARL E. MILLER[1] AND JOHN A. SMALLWOOD[1,2]

ABSTRACT.—Sex-biased natal dispersal is common among many bird species, with females usually dispersing farthest. The relative dispersal distances of male and female American Kestrels (*Falco sparverius*) are unknown. We examined natal dispersal in Southeastern American Kestrels (*F. s. paulus*) in north-central Florida, observing birds marked as nestlings with either color bands or patagial tags. Natal dispersal distances of 34 kestrels ranged from 0.0 to 38.8 km. Mean natal dispersal distance of females (8.6 km) did not differ significantly from that of males (8.3 km) ($P = 0.43$). We determined that no relationship existed for either sex between dispersal distance and subsequent reproductive success. However, the relationship between hatching date and dispersal distance was marginally significant ($P = 0.071$); fledglings from earlier nests were more likely to breed close to their natal area than were those from late-season nests. Our results suggest that natal dispersal and site fidelity in Southeastern American Kestrels are determined, at least in part, by inter- and intra-sexual competition for breeding sites. *Received 28 June 1996, accepted 11 Dec. 1996.*

Sex-biased dispersal is common among many bird species, with females usually the sex which disperses farthest (Greenwood 1980). Females may disperse farther than males as a result of a resource-defense system, whereby males typically defend breeding territories and females choose among many males (Greenwood 1980, Greenwood and Harvey 1982, Pusey 1987). The resource-defense hypothesis assumes that males settle close to their natal area because prior familiarity with the area facilitates the establishment of territories. Social constraints may dictate that males continue to exhibit fidelity to breeding sites because of the importance of familiarity with their neighbors in establishing and defending territories (Payne and Payne 1993).

The relative dispersal distances of male and female American Kestrels (*Falco sparverius*) are unknown. However, given the fact that the male of the species establishes and defends the breeding territory (Balgooyen 1976), we might expect that dispersal would be female-biased. In migratory populations of American Kestrels (*F. s. sparverius*), males return to the breeding ground earlier than females (Bird and Palmer 1988), allowing them the opportunity to establish territories before females return. If females benefit from the opportunity to choose among many males and

[1] Dept. of Wildlife Ecology and Conservation, Univ. of Florida, P.O. Box 110430, Gainesville, Florida 32611.
[2] Present address: Dept. of Biology, Montclair State Univ., Upper Montclair, New Jersey 07043.

the resources they provide (e.g., through courtship feeding; Balgooyen 1976), we would then expect females to exhibit greater natal dispersal than males.

More studies are needed to examine the asymmetries in cost-benefits of dispersal in birds. Pusey (1987) suggested that by measuring breeding success of males and females at different distances from the natal area, hypotheses about the costs and benefits of natal dispersal could be tested.

We examined natal dispersal in nonmigratory Southeastern American Kestrels (*F. s. paulus*) in north-central Florida. The southeastern race, resident in Florida, has declined and is listed as threatened in Florida (Hoffman and Collopy 1988, Collopy 1996). We hypothesized that (1) natal dispersal distances would be greater for females than for males and that (2) female dispersal distance would be positively correlated with subsequent breeding success, whereas male dispersal distance would be negatively correlated with subsequent breeding success.

STUDY AREA AND METHODS

Nest boxes (N = 347) were erected in north-central Florida in 1990 and 1991 as part of a population study (Smallwood and Collopy 1993). The study site was approximately 1200 km^2 in area and included portions of Alachua, Levy, and Marion counties. Nest boxes were mounted on live trees and on Florida Power Corporation utility poles in proximity to suitable foraging habitat (open areas with grasses and weedy forbs <25 cm in height; Smallwood 1988). Most nest boxes were located in remnant longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) sandhills or in pastures and agricultural habitats. Kestrel populations in these habitats were low prior to the initiation of the study due to a decline in the availability of natural nest-sites (Hoffman and Collopy 1988). Nearest-neighbor distances between nest boxes ranged from 1 to 2 km in most areas, which reflected the typical spacing between territories reported for kestrel populations elsewhere in North America (Bird and Palmer 1988).

Nest boxes were monitored throughout the breeding season (late March through mid-July). Nests were visited two or more times during incubation to determine clutch size and expected hatching date, and again before fledging to band the young. Each nestling surviving to banding age (14–24 days) was banded with a single U.S. National Biological Service aluminum band on one tarsus and either a combination of two colored plastic bands on the other tarsus or a unique patagial tag on one wing. Not all color-banded chicks received unique band combinations. Color band combinations denoted range and township locations during 1991 and individual nest boxes in 1992. Beginning in 1992, individuals banded as chicks in 1991 were observed using nest box territories as adults. During each visit to nest boxes in 1992–94, we also recorded the location, sex, behavior, and color markings of any adults present. When a banded adult was encountered on a nest box territory, we made repeated visits to confirm its identity.

We defined natal dispersal as the movement of individuals to a potential breeding site irrespective of whether they reproduced after dispersal (i.e., as in gross dispersal, Greenwood 1980). Natal dispersal was measured as the straight-line distance between the nest box where the kestrel hatched and the nest box where it was observed the following breeding season. In the two instances where color markings observed were not unique to a specific natal site, the median distance to all possible natal sites was used for analyses. Locations of all nest

TABLE 1
NATAL DISPERSAL DISTANCES (KM) OF MALE (N = 13) AND FEMALE (N = 21) COLOR-MARKED SOUTHEASTERN AMERICAN KESTRELS IN NORTHCENTRAL FLORIDA, 1992–1994

	Male	Female
Range	0.00–32.45	2.14–38.79
Mean (SE)	8.28 (2.58)	8.60 (1.76)
Median	4.38	5.06

boxes were determined with a portable global positioning system (Trimble Navigation, Sunnyvale, California). Locations were recorded in latitude/longitude and then converted to Universal Transverse Mercator coordinates. Dispersal distance was then calculated as the straight-line distance (hypotenuse) between the two points. Dispersal data were not normally distributed; therefore, non-parametric statistical treatments were used for all tests of significance.

Marked adults were considered to have bred at a particular nest box if they were observed making territorial displays (vocalizing, perching near, or flying close to the observers) while eggs or chicks were present in the nest box. The relationships between hatching date, dispersal distance, and the number of young fledged in their first breeding attempt were tested with Spearman's correlations.

RESULTS

Fifty color-marked adult kestrels, including 34 one-year-old birds, were observed on nest box territories during the breeding seasons of 1992–1994. Natal dispersal distances of the 34 kestrels ranged from 0.0 km (a male that inherited his father's breeding territory as a yearling) to 38.8 km (Table 1). Most (71%) individuals dispersed <8 km (median distance = 4.9 km), while only a few dispersed much greater distances.

The distribution of male dispersal distances was similar to that of females (Fig. 1). Mean natal dispersal distance of males (8.3 km) did not differ significantly from that of females (8.6 km) (Wilcoxon rank-sum test, $Z = -0.797$, $P = 0.43$). When data were pooled into near (0–8 km) and far (>8 km) categories, no significant difference was detected between sex and distance (Fisher's exact test, $P = 0.70$).

Egg-laying was confirmed for 28 (82%) of 34 one-year-old kestrels. The number of fledged young at these nests ranged from none to five and was not correlated significantly with natal dispersal distance for either males ($r_s = 0.062$, $P = 0.88$) or females ($r_s = -0.049$, $P = 0.84$). When data for both sexes were combined, the relationship between an individual's hatching date and its subsequent dispersal distance approached statistical significance ($r_s = 0.323$, $P = 0.071$).

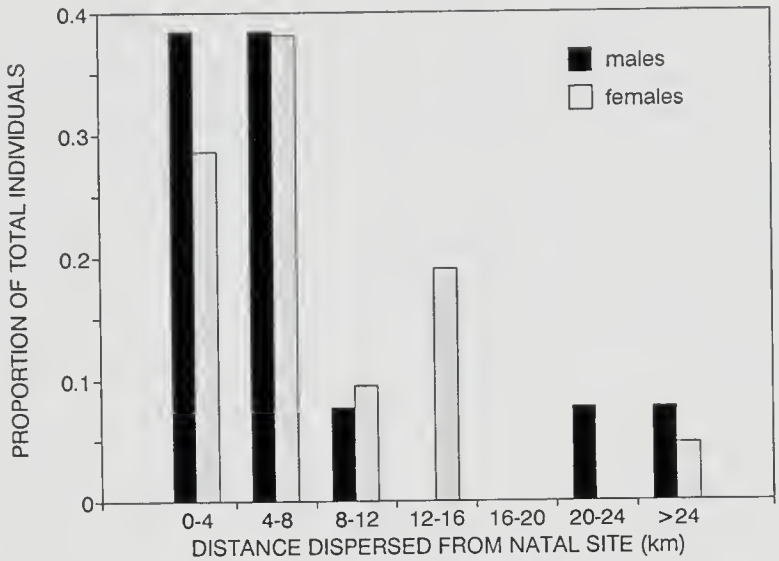

FIG. 1. Distribution of natal dispersal distances for Southeastern American Kestrels (N = 13 males and 21 females).

DISCUSSION

American Kestrels exhibited a skewed dispersal pattern, with most individuals dispersing relatively short distances, and a few dispersing much greater distances. A similar pattern has been reported for other raptor species, including Eurasian Sparrowhawks (*Accipiter nisus*) (Newton and Marquiss 1983, Newton 1986), Ospreys (*Pandion haliaetus*) (Doig 1989, Johnson and Melquist 1991), Eastern Screech-Owls (*Otus asio*) (Belthoff and Ritchison 1989), and Great Horned Owls (*Bubo virginianus*) (Adamcik and Keith 1978).

Despite dispersing relatively short distances, most kestrels bred outside their natal home range. American Kestrel breeding territories are typically small (e.g., 0.24 km^2, Bowman et al. 1987; 0.82 km^2, Smith et al. 1972), with a diameter of usually no more than 1.0–2.5 km (Bird and Palmer 1988). Although we did not measure individual territory size in the present study, it is likely that nearly all individuals dispersed outside their natal home range (94% dispersed ≥3 km). One notable exception was a yearling male kestrel that successfully bred in the same nest box from which it fledged. It is not known whether he bred with his mother or an unrelated adult female because the adult female at the site was not color-marked. However, close inbreeding in kestrels has been recorded in a banding study in Canada, where a father-daughter pair bred and raised young successfully (D. Bird, pers. comm.).

We did not observe sex-biased natal dispersal. Much of the evidence for female-biased dispersal in raptors is from regional studies of eagles

or Ospreys. For example, in a study of Ospreys along the New England coast, Spitzer et al. (1983) found that 64% of females and 27% of males dispersed ≥10 km from their natal site; the maximum movement of females was 520 km in contrast to only 37 km for males. Comparisons of male and female dispersal distances in such a wide-ranging species would be biased if such a study were conducted in a restricted geographical area because the long distance movements of females would go undetected. However, it is unlikely that the spatial constraints of our study biased our comparison of male and female natal dispersal distances in kestrels because nest boxes were 1–2 km apart and the diameter of our study area was 30–50 km. Moreover, female-biased natal dispersal has been documented for raptors in study areas much smaller than ours, including a 36-km^2 study of Burrowing Owls (*Athene cunicularia*) (Millsap and Bear 1993) and a 122-km^2 study of Merlins (*Falco columbarius*) (James et al. 1987, but see James et al. 1989).

We determined that no significant relationship existed between dispersal distance and the subsequent number of young fledged. If we regard the number of offspring reared as an index of fitness, then our findings suggest no direct relationship between fitness and dispersal distance. The relationship between hatching date and dispersal distance approached statistical significance ($P = 0.071$), lending more support to the alternative hypothesis that dispersal distance is a function of competition for available breeding sites. Waser (1985) suggested that early dispersers may settle closer to their natal territories because they are able to choose the closest vacant territories, whereas late dispersers must move farther away to find suitable sites. Village (1990) found late broods of Eurasian Kestrels (*Falco tinnunculus*) dispersed farther than earlier broods and were more likely to have reduced winter survival. He posited that juveniles move away from the nest until they locate a vacant territory where they are not driven away by adults or other juveniles. In contrast, there was no correlation between hatching date and dispersal distance in Eurasian Sparrowhawks (Newton and Marquiss 1983) or Boreal Owls (*Aegolius funereus*) (Korpimaki and Lagerstrom 1988), and no correlation between dispersal date and dispersal distance in Eastern Screech-Owls (Belthoff and Ritchison 1989). However, Eurasian Sparrowhawks that dispersed farthest from their natal site subsequently bred in poorer habitat, initiated nesting later in the season, and produced smaller clutches (Newton and Marquiss 1983), a result consistent with the hypothesis that subordinate or less competitive individuals are forced to move away from the natal area.

Shields (1982) defined philopatry as returning to an area within 10 home ranges of the natal site. Given this definition, philopatry of Amer-

ican Kestrels in our study area is probably quite high (71% if home range diameters are 1.0 km, 94% if home range diameters are 2.5 km). Similarly, in a Wisconsin study area supplemented with nest boxes, seven of 10 kestrels recaptured or recovered in subsequent breeding seasons were encountered within 35 km of their natal area (Jacobs 1995). Data from long-term banding projects in Canada suggest that migratory American Kestrels are "loosely philopatric," with most individuals returning to the same general area but rarely to the same nest site (Bowman et al. 1987). Our data show philopatry may be stronger for resident Southeastern American Kestrels in Florida. It is possible that the availability of nest boxes throughout the study area decreased the modal dispersal distance.

Our data also suggest that competition for nest sites may be more important than sex in determining the extent of natal dispersal in this population. Fledglings from late nests may be forced to disperse farther from their natal area than fledglings from early nests, regardless of sex. However, the timing of dispersal events in this nonmigratory population is not precisely known. More information on the seasonal timing of natal dispersal may further substantiate the relationship between hatching date, dispersal date, natal dispersal distance, and philopatry.

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NESTING SUCCESS OF KENTUCKY AND HOODED WARBLERS IN BOTTOMLAND FORESTS OF SOUTH CAROLINA

ROBERT A. SARGENT,[1] JOHN C. KILGO,[2] BRIAN R. CHAPMAN,[2] AND KARL V. MILLER[2]

ABSTRACT.—We studied the nesting success of Kentucky Warblers (*Oporornis formosus*) and Hooded Warblers (*Wilsonia citrina*) in 15 bottomland hardwood forests on the Savannah River Site, South Carolina, during 1993–1994. The Mayfield success rate for Kentucky Warbler nests (N = 26) and Hooded Warblers nests (N = 33) was 34.7% and 28.7%, respectively. The daily survival rate for Kentucky Warbler nests (0.952, SE = 0.018) did not differ ($P = 0.157$) from that for Hooded Warbler nests (0.941, SE = 0.014). Successful Kentucky Warbler pairs fledged more ($P < 0.001$) young (3.7, SE = 0.2) than Hooded Warbler pairs (2.7, SE = 0.2). Hatch-year birds comprised a greater ($P < 0.01$) proportion of captured individuals for Kentucky Warblers (hatch-year:after-hatch-year = 2.2) than for Hooded Warblers (hatch-year:after-hatch-year = 0.4), possibly reflecting the greater number of young produced per successful nest for the former, and suggesting differences in post-fledging survival or in fledgling behavior between the species. *Received 17 May 1996, accepted 7 Dec. 1996.*

Bottomland hardwood forests support some of the highest bird densities in the southeastern United States (Dickson 1978). Many of the priority species of the Partners in Flight priorization scheme, including Kentucky Warblers (*Oporornis formosus*) and Hooded Warblers (*Wilsonia citrina*), rely on these forests as breeding and stopover habitat (Hunter et al. 1993a, 1993b). Both of these warblers inhabit the understories of moist deciduous forests in the region and are considered forest-interior specialists (Sprunt and Chamberlain 1949, Whitcomb et al. 1981). Hooded Warblers generally nest in low shrubs (Kilgo et al. 1996a) and forage within 5 m of the ground, whereas Kentucky Warblers nest (Kilgo et al. 1996b) and forage near ground level (Powell and Rappole 1986). Our objective was to quantify the nesting success rates of these two warblers in various-sized bottomland hardwoods on the Savannah River Site (SRS), South Carolina, and to identify the factors that limited nesting success.

STUDY AREA AND METHODS

Study sites were on the 77,891-ha SRS in the upper coastal plain of South Carolina. Bottomland hardwood forests (N = 15) ranged in width from <50 m to >1000 m and were bordered by extensive mature pine forest (*Pinus taeda* and *P. palustris*). Bottomland over-

[1] WR-ALC/EMX, 216 Ocmulgee Ct., Robins Air Force Base, Georgia 31098.
[2] D.B. Warnell School of Forest Resources, Univ. Georgia, Athens, Georgia 30602.

stories were dominated by sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), and swamp tupelo (*Nyssa sylvatica* var. *biflora*). Dominant mid-story species included American holly (*Ilex opaca*), red bay (*Persea borbonia*), and ironwood (*Carpinus caroliniana*), and the understory species consisted of switchcane (*Arundinaria gigantea*), dog-hobble (*Leucothoe axillaris*), and Christmas fern (*Polystichum acrostichoides*).

We searched each site for nests every 1–2 weeks during May–July 1993 and 1994. Time expended searching each site was proportional to the average width of that site (i.e., twice as much time was expended searching for nests in a 300-m-wide bottomland as was spent searching in a 150-m-wide bottomland). We monitored the status of each nest following the procedures of Martin and Geupel (1993). We used the techniques of Best and Stauffer (1980) to assess the outcome of each nesting attempt. We calculated the daily survival rates (DSR) of nests and Mayfield success rates (Mayfield 1961, 1975). We assumed that the nest survival rates for the incubation and nestling intervals were similar within species because sample sizes were limited (Klett and Johnson 1982). Differences in nest DSRs between species were tested with a two-tailed *Z*-test. We compared Mayfield nest success rates between species using 2 × 2 Chi-square contingency tables. Student's two-sample *t*-test was used to compare the number of young fledged per successful nest between species.

We captured birds in mist nets in 11 of these sites during 7 July–29 July 1994. In each site, 10 nets (2.5 × 10 m, 30 mm mesh) were deployed along the center of the corridor, one every 30 m. We netted each site for two consecutive days, removed the nets for two weeks, then repeated the procedure. We banded each bird and aged them by their plumage, molt, skull pneumatization, or reproductive condition (Pyle et al. 1987). We calculated hatching-year (HY) to after-hatching-year (AHY) ratios for Kentucky and Hooded warblers as an additional index of reproductive success (Ralph et al. 1993). Recaptures were not included in the HY:AHY analysis. We compared the proportion of captured HY individuals between species using 2 × 2 Chi-square contingency tables.

RESULTS

Mean hatch and fledge dates for Kentucky Warbler nests were 4 June (N = 22; range = 17 May–10 July) and 14 June (N = 19; range = 26 May–19 July), respectively. The corresponding dates for Hooded Warbler nests were 13 June (N = 26; range = 11 May–20 July) and 24 June (N = 17; range = 19 May–29 July), respectively. Nests of both warblers generally were found in bottomlands averaging ≥300 m in width (Kentucky Warbler nests = 61.5%; Hooded Warbler nests = 66.7%). However, both species successfully fledged young in smaller sites, even bottomlands <50 m in width.

Successful Kentucky Warbler pairs fledged more ($t = 3.92$, $P < 0.001$, 34 df) young (3.7, SE = 0.2) than did successful Hooded Warbler pairs (2.7, SE = 0.2) (Table 1). Nest success rates did not differ ($\chi^2 = 0.052$, $P > 0.05$) between species. Daily survival rates for the nesting cycle were 0.952 for Kentucky Warblers and 0.941 for Hooded Warblers and were not significantly different ($Z = 0.482$, $P = 0.157$).

No Kentucky Warbler nests were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Six (18.2%) Hooded Warbler nests were parasitized, containing an average of 1.2 cowbird eggs (Table 1). Host young

TABLE 1

PRODUCTIVITY ESTIMATES FOR KENTUCKY WARBLERS AND HOODED WARBLERS IN BOTTOMLAND HARDWOOD FORESTS ON THE SAVANNAH RIVER SITE, SOUTH CAROLINA, 1993–1994

Parameter	Kentucky Warbler	Hooded Warbler
Active nests	26	33
Mean clutch size	4.2 (6; 0.4)[a]	3.0 (14; 0.0)
Young fledged/successful nest	3.7 (19; 0.2)	2.7 (17; 0.2)
Mayfield success rate (%)	34.7 (145)[b]	28.7 (272)
Daily survival rate	0.952 (0.018)[c]	0.941 (0.014)
Nests parasitized by cowbirds	0	6
Cowbird eggs/parasitized nest		1.2 (0.2)[c]
Host eggs/parasitized nest		1.7 (0.2)

[a] Sample size and standard error.
[b] Number of nest exposure days.
[c] Standard error.

successfully fledged from just one of these parasitized nests. Predation accounted for 87% of nest failures, including all Kentucky Warbler nest failures, and 81.3% of Hooded Warbler nest failures (Table 2). Mayfield-corrected nest depredation rates were 65.3% and 57.9% for Kentucky Warblers and Hooded Warblers, respectively. Most depredated nests were found empty and undisturbed.

Excluding recaptures, we netted 47 Hooded Warblers and 29 Kentucky Warblers, representing the most- and third-most abundant species captured in these sites. Hatch-year birds comprised a greater proportion ($\chi^2 = 9.61$, $P < 0.01$) of captures for Kentucky Warblers (HY:AHY = 2.2) than for Hooded Warblers (HY:AHY = 0.4). No cowbirds were netted.

TABLE 2

PROBABLE CAUSES (%)[a] OF NESTING FAILURE FOR KENTUCKY WARBLERS AND HOODED WARBLERS IN BOTTOMLAND HARDWOOD FORESTS ON THE SAVANNAH RIVER SITE, SOUTH CAROLINA, 1993–1994

Nest outcome	Kentucky Warbler	Hooded Warbler
Success	73	52
Predation: nest undisturbed	23	27
Predation: nest disturbed	4	12
Cowbird parasitism[b]	0	3
Abandoned	0	3
Weather	0	3

[a] Apparent nest percentages.
[b] Only nests for which failure could be attributed solely to parasitism.

DISCUSSION

Robinson (1992) reported a Mayfield success rate of 22% (N = 3 nests) for Kentucky Warbler nests in small Illinois woodlots. Martin (1992), in a review of nest studies conducted in a variety of habitats, reported a mean Mayfield success rate of 42% and a mean apparent success rate of 44%. Mayfield nest success rates from our study were low by comparison, particularly for Hooded Warblers, while apparent success rates were relatively high. Although our data were below average productivity estimates for these species elsewhere, the paucity of nest success data from the southeastern United States for Kentucky Warblers and Hooded Warblers renders our conclusions tenuous.

The HY:AHY ratios were higher than those of Neotropical migrants captured in small (i.e., <65 ha) Illinois woodlots (but see Bollinger and Linder 1994) and were within the range of ratios (0.4-1.0; total HY:AHY = 0.1) reported for much larger forests in southern Illinois (Robinson 1992). Hatch-year Kentucky Warblers proportionally were more common in our bottomland sites than were HY Hooded Warblers, suggesting that Kentucky Warblers had greater reproductive success. Because the Mayfield analysis indicated similar reproductive success for these species, differences in the proportion of HY birds may be explained, in part, by the greater mean clutch sizes of Kentucky Warbler nests. Differences in the proportion of HY birds also may be due to dissimilar post-fledging survival or dissimilar fledgling behavior (i.e., Kentucky Warbler fledglings may have been more susceptible to capture), or may reflect differences in the frequency of double brooding between the species.

Predation appears to have been the principal cause of nesting failure in our study, as frequently reported elsewhere (Martin 1992). Stutchbury and Howlett (1995) reported annual nest depredation rates of 38.3% to 50% for Hooded Warblers in northwestern Pennsylvania. The mean depredation rate for Hooded Warbler nests (57.9%) in this study was similar to these results. The depredation rate for Kentucky Warbler nests (65.3%) also was comparable to most studies (Martin 1992, Robinson 1992) but was high relative to nest depredation rates for ground-nesting warblers in upland hardwoods of Arkansas (Martin 1993).

Nests of these warblers commonly are parasitized by Brown-headed Cowbirds in the midwestern and northeastern United States (Friedmann 1963, Evans Ogden and Stutchbury 1994). Brood parasitism rates were moderate for Hooded Warbler nests in this study, and no parasitism was observed for Kentucky Warbler nests. The Brown-headed Cowbird is considered an uncommon species in the SRS region in summer (Norris 1963, Post and Gauthreaux 1989). The lack of cowbirds captured during netting,

and the dearth of observations of this species during a concurrent census study (J. C. Kilgo, unpubl. data), suggest that cowbirds are uncommon in these bottomland sites.

Robbins (1979) estimated that 30 ha was the minimum area required to sustain viable populations of Hooded and Kentucky Warblers in Maryland woodlots. Although both species successfully reproduced in small bottomlands in this study, including sites <50 m in width, all of our sites were enclosed by mature pine forest. This mature timber habitat minimized edge contrast and may have increased the functional size of the bottomland forests, thereby improving the suitability of these sites as nesting habitat for these warblers (Harris 1984). Further research is needed regarding the value of the forest matrix for songbirds nesting in riparian forests. Maintenance of riparian forests in landscapes dominated by a pine forest matrix appears to be essential to the conservation of Kentucky and Hooded Warblers in the southeastern U.S.

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EFFECT OF CLEARCUT BORDERS ON DISTRIBUTION AND ABUNDANCE OF FOREST BIRDS IN NORTHERN NEW HAMPSHIRE

DAVID I. KING,[1] CURTICE R. GRIFFIN,[1] AND RICHARD M. DEGRAAF[2]

ABSTRACT.—We compared numbers of forest bird territories between forest edge and forest interior areas to determine whether clearcuts affect bird abundance in adjacent forest. We then simulated the distribution of territories that would be expected if birds were neither attracted to nor repelled by clearcut borders by randomly locating 100 1-ha circular "simulated" territories on scale maps of the study plots, with the condition that simulated territories were located entirely within mature forest. Plots were divided into successive 50-m distance classes extending from clearcut borders 300 m into forest interior, and the distribution of territories of each species among 50-m distance classes was compared with the distribution of simulated territories. Red-eyed Vireos (*Vireo olivaceus*) and Hermit Thrushes (*Catharus guttatus*) were less abundant in edge areas, but the distribution of these species did not differ from the distribution of randomly placed simulated territories. We conclude that lower abundance of forest birds in edge areas is not necessarily evidence of edge avoidance but may be merely the result of the absence of suitable habitat beyond clearcut borders. *Received 27 Feb. 1996, accepted 20 Nov. 1996.*

Forest fragmentation is an important factor in the decline of many populations of forest-dwelling Neotropical migrant birds (Robinson et al. 1995). A phenomenon associated with the process of forest fragmentation is an increase in the proportion of the remaining habitat consisting of edge (Temple 1986). Edges affect forest birds in a number of ways. Some forest bird species appear to avoid edges, possibly because of changes in vegetation structure (Gates and Gysel 1978, Strelke and Dickson 1980, Kroodsma 1984) or because of high rates of nest predation near edges (Gates and Gysel 1978, Temple and Carey 1988, King et al., in press). In this study, we tested whether clearcutting affected the abundance of birds in forest adjacent to clearcuts by comparing numbers of forest bird territories between edge and forest interior areas.

Lower abundance of forest birds near edges is generally interpreted as evidence of edge avoidance; however, it has been suggested that lower abundance of forest birds could result from the restriction of these species to mature forest habitat rather than active edge avoidance (Kroodsma 1984, Rich et al. 1994). Therefore, we simulated the distribution of territories that would be expected if forest birds were restricted to mature

[1] Dept. of Forestry and Wildlife Management, Univ. of Massachusetts, Amherst, Massachusetts 01003.
[2] USDA Forest Service Northeast Forest Experiment Station, Univ. of Massachusetts, Amherst, Massachusetts 01003.

forest but otherwise located territories at random with respect to clearcut borders. Observed distributions of forest bird territories were compared with the distribution of simulated territories to test if there was evidence of active edge avoidance or if distributions of forest bird territories relative to clearcut borders could be explained by the restriction of these species to mature forest habitat.

STUDY AREA AND METHODS

Four study plots were established in mature (≥80 yrs old) northern hardwoods forest adjacent to three recent (≤6 yrs) clearcuts on the Saco District of the White Mountain National Forest in northern New Hampshire (44°03′N, 71°15′W). Bird territories were mapped on each plot using a modified spot-mapping technique (Holmes and Sturges 1975): Two skilled observers walked slowly (1.2 km-h^{-1}) along parallel transects placed 100 m apart, recording the species and location of all birds seen or heard on scale maps of the study plots. Each transect extended from 50 m within the clearcut, across the clearcut border, and 350 m into the forest interior. Surveys were conducted within 1.5 h of sunrise, and both the direction transects were walked and the observers were alternated among surveys. Eight transect counts were conducted on each plot between May and August in 1992 and 1993. Bird data were transferred onto transparent drafting film. A polygon connecting a cluster of three or more observations of an individual was designated as a territory of that species, and evidence of counter singing was used to separate adjacent territories (Robbins 1970). Only species for which ≥10 territories were mapped were included in the analyses (Strelke and Dickson 1980).

We compared the number of territories of individual bird species between 0–100 m (hereafter "edge areas") and 200–300 m (hereafter "interior areas") from clearcut borders using G-tests (Zar 1984:77). Data collected between 300–350 m were not analyzed to avoid the inclusion of partially mapped territories. Additionally, we simulated the distribution of territories that would be expected if forest birds were locating their territories randomly in relation to clearcut borders by drawing 100 1-ha circular territories at randomly located points on scale maps of the study areas, with the condition that territories were situated entirely within mature forest. (1-ha territories correspond to the territory size of many common Neotropical migrant bird species present on our study sites; DeGraaf and Rudis 1986). Study plots were divided into successive 50-m distance classes extending from clearcut borders 300 m into forest interior. The distribution of actual territories was compared with the distribution of simulated territories using the Kolmogorov-Smirnoff goodness-of-fit test (Zar 1984:53). The number of simulated territories was also compared between edge and interior areas using G-tests, after scaling the number of simulated territories equal to the total number of the most abundant bird species in our study. This procedure eliminated the possibility that differences in number of simulated territories between edge and interior areas might be a result of increased statistical power due to large sample size (N = 100 simulated territories). The distribution of forest bird territories among 50-m distance classes was compared between years using the Kolmogorov-Smirnoff goodness-of-fit test. No significant differences were detected ($p > 0.10$), so data were pooled between years.

Average tree height, average canopy height, percent canopy cover, percent herbaceous cover, shrub density and tree basal area were measured on 80 randomly located 0.04-ha circular plots (Noon 1981). Two 22.3-m long transects were established on each plot, oriented in the cardinal directions and intersecting the plot center. The tree closest to the plot center in each of the four quadrants formed by the intersection of the two transects was

TABLE 1

NUMBER OF BIRD TERRITORIES IN EDGE AND INTERIOR AREAS

	Edge	Interior	*G*	df	*P*
Red-eyed vireo (*Vireo olivaceus*)	9	18	3.20	1	0.07
Ovenbird (*Seiurus aurocapillus*)	11	12	0.00	1	1.00
Black-throated Green Warbler (*Dendroica virens*)	5	8	0.50	1	0.48
Black-throated Blue Warbler (*D. caerulescens*)	10	2	5.78	1	0.02
American Redstart (*Setophaga ruticilla*)	4	4	0.00	1	1.00
Scarlet Tanager (*Piranga rubra*)	4	7	0.84	1	0.36
Hermit Thrush (*Catharus guttatus*)	2	8	3.74	1	0.05
Simulated Territories	8.4	19.2	4.34	1	0.04

selected and the height of the crown and lowest branch in the canopy were measured in meters using a clinometer. Percent canopy and herbaceous cover were measured at 20 regularly spaced intervals along the two transects using a sighting tube (Noon 1981). Shrub density at breast height was estimated by counting the number of stems ≤3 cm dbh contacting the outstretched arms and body of an observer walking the length of the two transects and multiplying the result by 125 to convert to stems-ha^{-1} (Noon 1981). Basal area (in m^2-ha^{-1}) was estimated on each plot for all species combined and for conifers considered separately using a ten-factor prism. Habitat variables were log transformed where necessary to improve normality and equality of variances (Zar 1984:238) and compared between edge and interior areas using two-sample *t*-tests (Zar 1984:126). Statistical analyses were done using STATISTIX (1992, Analytical Software Inc.). Statistical significance was set at P = 0.10.

RESULTS

Seven bird species were included in the analyses (scientific names in Table 1). Red-eyed Vireos and Hermit Thrushes were significantly less abundant in edge areas than forest interior areas. Black-throated Blue Warblers were significantly more abundant in edge areas than forest interior areas. Numbers of Ovenbirds, Black-throated Green Warblers, American Redstarts, and Scarlet Tanagers did not differ significantly between edge and interior areas. Simulated territories were less abundant in edge areas (Table 1).

The distribution of territories of four bird species did not differ from the distribution of randomly placed simulated territories (Fig. 1): Red-eyed Vireo (D = 0.13, P = 0.92, N = 45), Ovenbird (D = 0.18, P = 0.62, N = 37), Black-throated Green Warbler (D = 0.14, P = 1.00, N = 24), and Hermit Thrush (D = 0.22, P = 0.48, N = 13). In contrast, the distribution of territories of Black-throated Blue Warblers and American Redstarts were skewed significantly towards clearcut borders (D = 0.50, P = 0.004, N = 24; D = 0.53, P = 0.02, N = 24; Black-throated Blue Warblers and American Redstarts, respectively). The distribution of Scar-

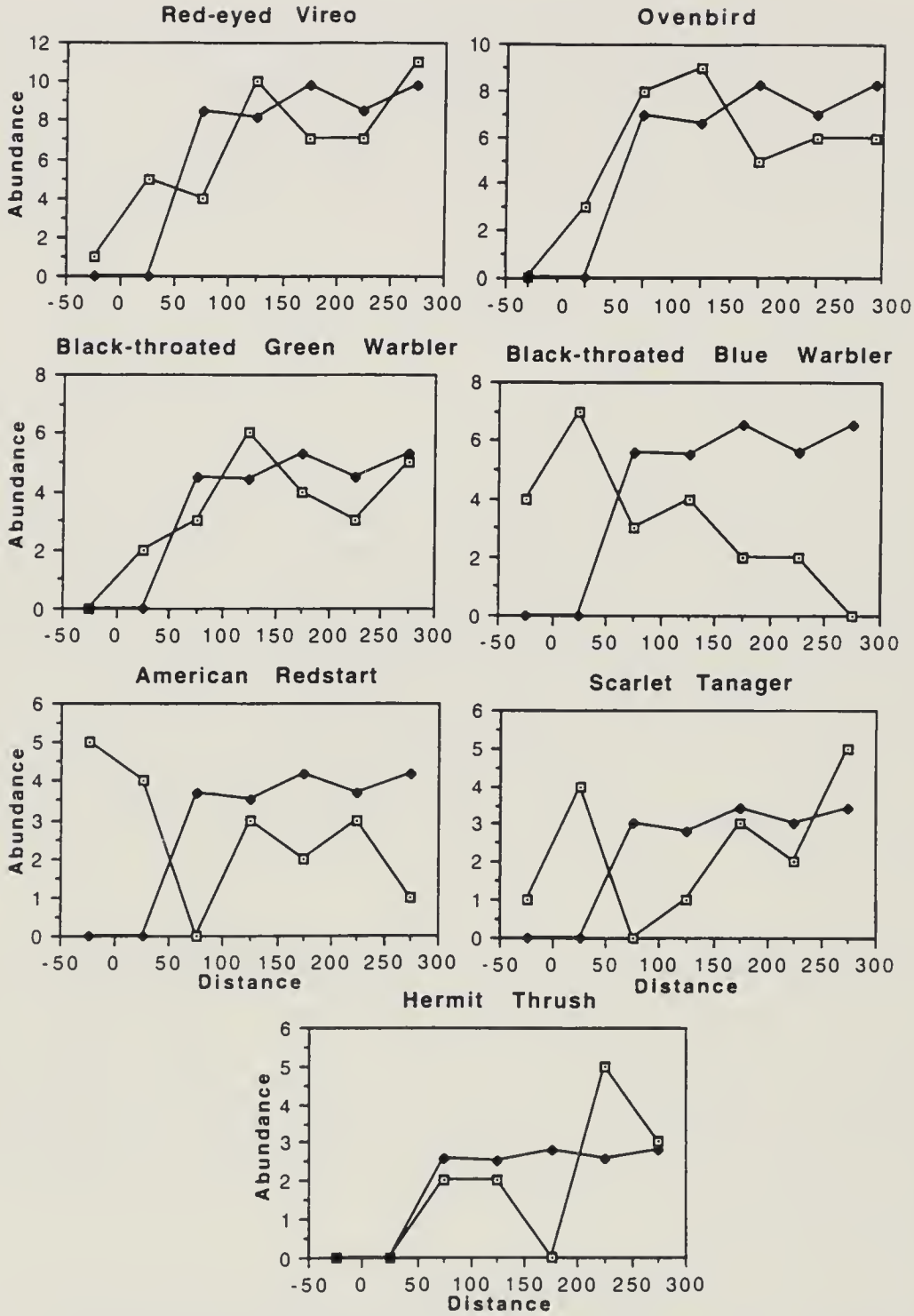

FIG. 1. Distribution of territories of forest bird species (open squares) compared with the distribution of simulated territories (black diamonds). Values on the X-axis represent successive 50-m intervals from 50 m within clearcuts to 300 m within forest interior.

let Tanager territories differed significantly from the distribution of simulated territories but was not clearly skewed towards either edge or interior ($D = 0.31$, $P = 0.08$, N = 16; Fig. 1).

Basal area, basal area of conifers, canopy cover, herb cover, canopy height, and tree height did not differ between edge and interior areas ($P > 0.10$). Shrub density was lower in edge areas ($t = 3.24$, $P = 0.002$, df = 78).

DISCUSSION

Various hypotheses have been advanced to explain lower abundance of forest birds near edges. One proposal is that forest birds actively avoid edges because of high rates of nest predation in these areas (Gates and Gysel 1978, Temple and Carey 1988, King et al., in press). However, it is unlikely that birds in regions where disturbance has been historically uncommon (such as our study area; Hornbeck and Leak 1991) have had the opportunity to evolve edge avoidance behavior (Kroodsma 1984, Ratti and Reese 1988, Van Horn et al. 1996). Another possibility is that differences in bird abundance between edge and interior areas is the result of changes in vegetation structure near edges (Gates and Gysel 1978, Strelke and Dickson 1980, Kroodsma 1984). However, according to published accounts of forest bird habitat use in our region (DeGraaf and Rudis 1986, Thompson and Capen 1988), there were no differences in vegetation parameters that would account for the differences we observed in Red-eyed Vireo and Hermit Thrush abundance between edge and interior areas.

An alternative explanation is that lower numbers of Red-eyed Vireo and Hermit Thrush territories in edge areas is an artifact of the restriction of these species to mature forest habitat. Rich et al. (1994) compared the abundance of forest bird species between forest edge and forest interior areas and concluded that lower abundance of forest birds near edges was the result of the absence of suitable habitat beyond edges rather than active edge avoidance. A similar explanation was proposed by Kroodsma (1984) to account for the displacement of forest bird territories away from powerline right-of-ways in east Tennessee. We argue that for birds that are restricted to mature forest habitat, territory centers will be displaced away from edges the distance of the radius of the territory. The potential for this type of displacement to appear as active edge avoidance is further illustrated by our observation that randomly located simulated territories were significantly less numerous in edge areas. Furthermore, the only species which had distributions shifted towards clearcut borders (Black-throated Blue Warbler and American Redstart) were also the only species we observed regularly defending territories in clearcuts.

One potential criticism of our territory simulation is that forest bird territories may become compressed near clearcut borders, whereas we assumed that territories are round, on average. If simulated territories were elongated rather than round, with their long axes parallel to clearcut borders, differences in numbers of simulated territories between edge and interior areas would have been less pronounced and distributions among 50-m distance classes would have been less skewed away from clearcut borders. Although birds that favor edge habitats are reported to alter the shape of their territories near edges, forest dewelling birds do not generally exhibit this behavior (Johnston 1947, Whitcomb et al. 1981, Kroodsma 1984, King, unpubl. data). Therefore, it appears the use of circular territories in our simulation is valid, at least for heuristic purposes.

We conclude that lower abundance of forest birds near edges is not necessarily evidence that forest birds avoid edges. Nevertheless, many of the practical considerations for natural resource managers are the same, regardless whether patterns of forest bird territory distribution are due to active edge avoidance or not. Of more significance are the implications for research on edge effects and forest birds. An unambiguous demonstration that forest birds avoid edges is necessary before the mechanisms underlying edge avoidance in birds can be meaningfully addressed.

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SEASONAL SHIFTS IN THE EFFECTS OF WEATHER ON THE VISIBLE MIGRATION OF RED-TAILED HAWKS AT HAWK MOUNTAIN, PENNSYLVANIA, 1992–1994

BRYAN MARANSKY,[1] LAURIE GOODRICH,[2] AND KEITH BILDSTEIN[2,3]

ABSTRACT.— We used hourly counts of Red-tailed Hawks (*Buteo jamaicensis*) migrating at Hawk Mountain during the autumns of 1992, 1993, and 1994, to examine the possibility that the extent to which time of day and local weather parameters affected the numbers of birds seen at the site varied over the course of autumn migration. Data were analyzed separately for early-, mid-, and late-season periods of migration. High versus low winds, following versus opposing winds, low versus high relative humidity, and high versus low barometric pressure were associated with increased hourly passage rates of Red-tailed Hawks. Relative humidity had a greater effect during early-season migration. Wind speed and wind direction had greater effects during late-season migration. We suggest that shifts in the extent to which weather affects the numbers of Red-tailed Hawks seen at Hawk Mountain Sanctuary result from seasonal shifts in the species' dependence on thermal- versus slope-soaring. *Received 6 March 1996, accepted 20 Nov. 1996.*

Counts of migrating raptors at traditional raptor these sites suggest that time of day and local weather are associated with changes in the numbers of raptors counted at these sites (Haugh 1972, Kerlinger 1989). The extent to which such associations vary over the course of autumn migration—a period of considerable seasonal change in weather—remains unstudied.

In eastern North America, many Red-tailed Hawks (*Buteo jamaicensis*) breeding in northern areas migrate south each autumn. Migration begins in August and ends in December (Bednarz et al. 1990, Preston and Beane 1993). At Hawk Mountain Sanctuary, counts of several thousand Red-tailed Hawks (55 years [1934–1991] $\bar{x}$ = 3231 ± 19.0 [SE]) peak in late October or early November each year (Allen et al. 1996).

Haugh (1972) found that northerly winds, low temperatures, decreasing humidity, and increasing barometric pressure were associated with high counts of Red-tailed Hawks migrating past Hawk Mountain Sanctuary. Titus and Mosher (1982) reported that Red-tailed Hawks migrating through the region were affected by wind direction, wind speed, temperature, and day of year. Brinker and Erdman (1983) reported that Red-tailed Hawks migrating in Wisconsin were affected by wind drift (i.e.,

[1] 8 Mifflin Street, Lebanon, Pennsylvania 17046.
[2] Hawk Mountain Sanctuary, RR 2, Kempton, Pennsylvania 19529.
[3] Send reprint requests to KLB.

more birds were pushed to the shores of Lake Michigan during westerly winds).

Here, we use Hawk Mountain count data collected during 1992, 1993, and 1994, to (1) document the extent to which time of day, wind direction, wind speed, relative humidity, and barometric pressure affect hourly counts of Red-tailed Hawks at the site and (2) examine the extent to which such effects shift over the course of autumn migration. We discuss our results in terms of seasonal changes in weather during autumn migration.

METHODS

Migrating raptors have been counted at Hawk Mountain, eastern Pennsylvania (40°58′N, 75°59′W at 464 m ASL), since 1934. Currently, hourly counts are conducted each day (weather permitting) between 15 August and 15 December. Except when precipitation interrupts the count, coverage begins at 08:00 and ends at 17:00 EST (Bednarz et al. 1990, Allen et al. 1996).

Staff and volunteers recorded the numbers of Red-tailed Hawks flying past the Sanctuary from 15 August to 15 December in 1992, 1993, 1994. Hourly records of wind direction and wind speed, the latter using the Beaufort scale (Lincoln et al. 1982) also were recorded. Barometric pressure (mm Hg) and relative humidity (measured every three hours) were obtained from the National Weather Service Station at the Lehigh Valley Airport in Allentown, Pennsylvania, 34 km east of the site (NOAA 1992, 1993, 1994).

We analyzed data collected between 14 September and 28 November each year, the period during which 98% of all Red-tailed Hawks counted at the site between 1934 and 1986 were recorded (Bednarz et al. 1990). We divided this period into three relatively equal periods of 25–26 days each (14 September to 8 October, 9 October to 2 November, and 3 November to 28 November, i.e., early-, mid-, and late-season, respectively).

We considered winds of 20 km/h and above to be high winds, and classified wind direction as "following" (i.e., tail-winds from the WNW, NNW, NW, N, NNE, NE, ENE, or E) versus "opposing" (i.e., head-winds from the W, WSW, SW, SSW, S, SSE, SE, ESE), variable, or none. We classified relative humidity and barometric pressure as either high (all values above the above the median; i.e., >68%, >754 mm, respectively) or low (all values below the median; i.e., ≤68%, and ≤754 mm, respectively).

We modeled hourly counts of Red-tailed Hawks seen between 08:00 and 17:00 EST using SAS generalized linear model (Proc GLM) one-way and two-way ANOVAs in which the main effects consisted of a single weather parameter or hour (one-way ANOVAs) or a single weather parameter or hour and time of season and their interaction term (two-way ANOVAs) (SAS Institute 1988). Although hourly counts used in our analyses are not temporally independent, substantial hour-to-hour variability in the count data suggest considerable independence, overall.

Results were considered significant when analyses yielded probabilities of less than 0.05.

RESULTS

In 1992, 1993, and 1994, 2984, 3582, and 4140 Red-tailed Hawks, were counted at Hawk Mountain Sanctuary between 14 September and 28 November, during 602, 518, and 633 h of observation, respectively. Significant shifts in hourly counts of Red-tailed Hawks migrating past the site were associated with time of day, wind direction, wind speed, relative

TABLE 1

ONE- AND TWO-WAY ANALYSIS OF VARIANCE FOR HOURLY COUNTS OF MIGRATING RED-TAILED HAWKS AT HAWK MOUNTAIN, PENNSYLVANIA, 1992–1994

Model and source of variation	df	Sum of squares	Mean square	*F*-test	*P*
Model hour					
Hour	8	6394	799	3.37	0.0008
Model wind speed					
Wind speed	1	7285	7285	30.8	<0.0001
Model wind direction					
Wind direction	1	14,892	14,892	64.4	<0.0001
Model relative humidity					
Relative humidity	1	8206	8206	34.9	<0.0001
Model barometric pressure					
Barometric pressure	1	6194	6194	26.2	<0.0001
Model hour and time-of-season					
Hour	8	6828	853	3.66	0.0003
Time-of-season	2	26,445	13,222	58.8	<0.0001
Interaction	16	4484	280	1.25	0.22
Model wind speed and time-of-season					
Wind speed	1	6300	6300	28.2	<0.0001
Time-of-season	2	21,912	10,956	49.1	<0.0001
Interaction	2	2678	1338	6.00	0.0025
Model wind direction and time-of-season					
Wind direction	1	13,799	13,799	64.0	<0.0001
Time-of-season	2	27,421	13,710	63.6	<0.0001
Interaction	2	8113	4056	18.8	<0.0001
Model relative humidity and time-of-season					
Relative humidity	1	7563	7563	34.1	<0.0001
Time-of-season	2	22,371	11,185	50.4	<0.0001
Interaction	2	4088	2044	9.21	<0.0001
Model barometric pressure and time-of-season					
Barometric pressure	1	1539	1539	6.76	<0.0001
Time-of-season	2	22,146	11,073	48.7	<0.0001
Interaction	2	427	213	0.94	0.39

humidity, and barometric pressure (Table 1). Numbers of migrating Red-tailed Hawks increased around mid-day, were higher during periods of high versus low wind speeds, higher during following versus opposing winds, higher during low versus high relative humidity, and higher during high versus low barometric pressures (Fig. 1).

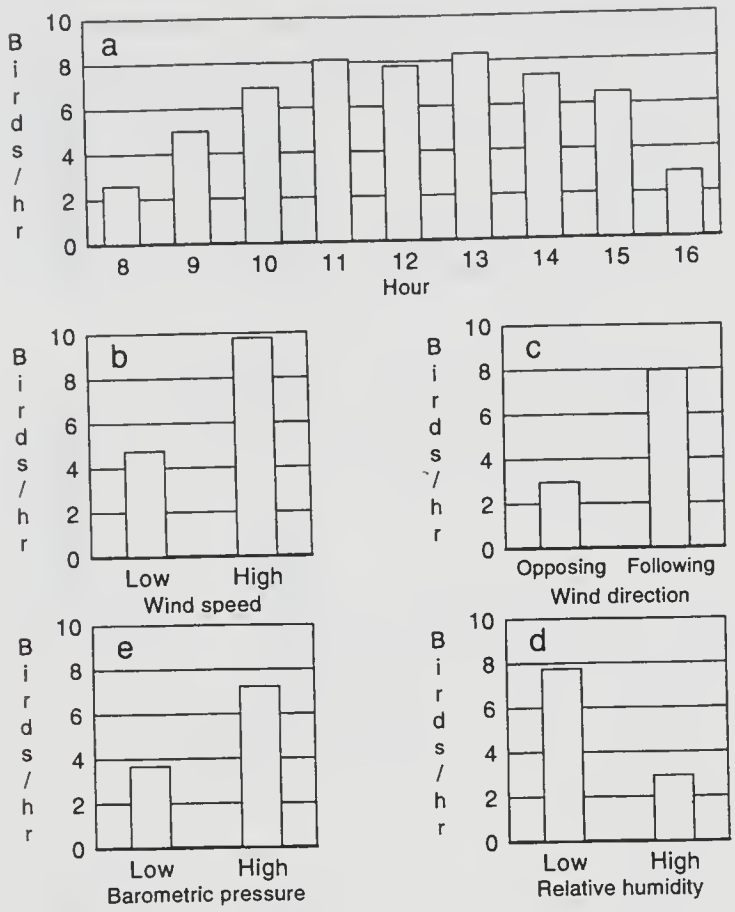

FIG. 1. Numbers of Red-tailed Hawks counted per hour of observation, 14 Sept.–28 Nov., 1992–1994, at Hawk Mountain Sanctuary, as a function of time (E.S.T) (a), low versus high wind speed (b), opposing versus following wind (c), low versus high relative humidity (d), and low versus high barometric pressure (e). See text for details regarding categories of weather parameters.

Our second series of analyses indicate significant interactions between time of season and wind direction (with a greater effect later in the season [i.e., ratios of counts on following versus opposing winds of 1.99:1, 2.24:1, and 3.12:1, during early, mid-, and late-season migration periods, respectively]), wind speed (with a greater effect later in the season [i.e., ratios of counts on low versus high winds of 1.26:1, 2.43:1, and 1.79:1, during early, mid-, and late-season migration periods]), and relative humidity (with a greater effect early in the season [i.e., ratios of counts during low versus high relative humidities of 4.77:1, 1.99:1, and 2.62:1, during early, mid-, and late-season migration periods]) but not between time of season and time of day or barometric pressure (Table 1; Fig. 2).

DISCUSSION

Evidence suggests that some species of birds vary their migratory behavior depending upon time of season (cf. O'Reilly and Wingfield 1995).

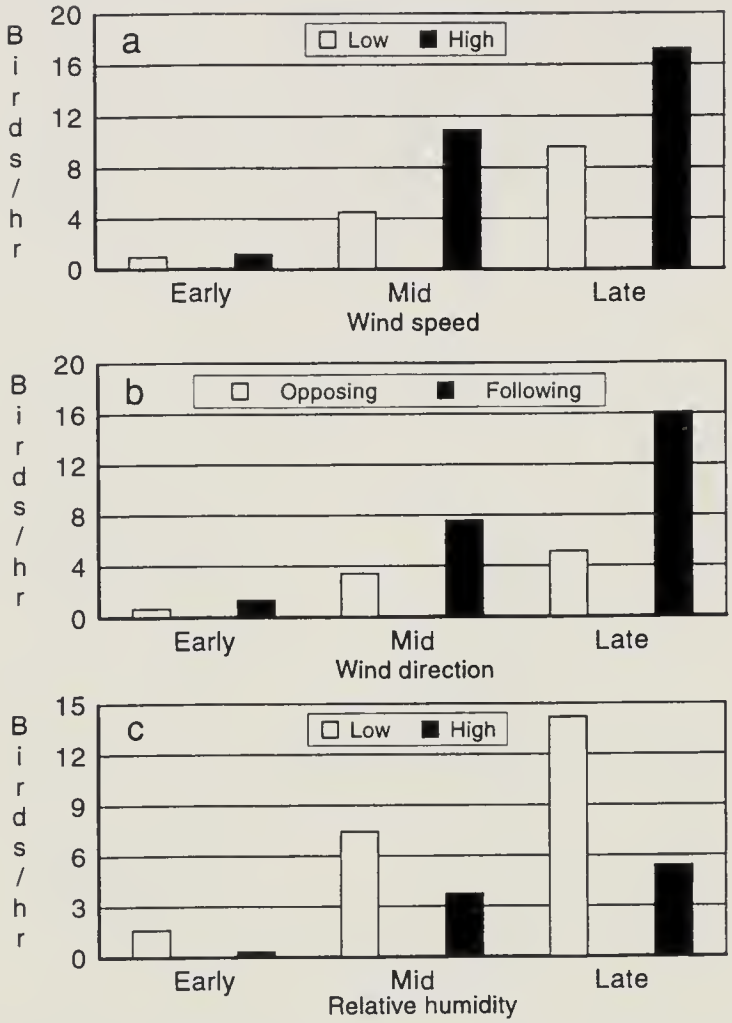

FIG. 2. Numbers of Red-tailed Hawks counted per hour of observation, 14 Sept.–28 Nov., 1992–1994 at Hawk Mountain Sanctuary as a function of wind speed (a), wind direction (b), and relative humidity (c) during early season (15 Sept.–8 Oct.) mid season (9 Oct.–2 Nov.), and late season (3–28 Nov.) migration periods. See text for details regarding categories of weather parameters.

Our results indicate that this may be true for Red-tailed Hawks migrating past Hawk Mountain Sanctuary.

Red-tailed Hawks typically engage in energy-saving slope and thermal soaring while migrating (Kerlinger 1989). An analysis of Hawk Mountain data from 1934 through 1991 (Allen et al. 1996) revealed that counts of Red-tailed Hawks increase significantly during the two days following the passage of cold fronts. At such times, temperatures moderate, fair skies reappear, following winds frequently occur, and thermals begin to form—the latter, especially, in August and September (Miller 1976).

At Hawk Mountain, Red-tailed Hawks migrate from mid September to late November (Bednarz et al. 1990), a period of considerable change in

TABLE 2

MEAN DAILY TEMPERATURES AND AMOUNTS OF DAYLIGHT HOURS AT ALLENTOWN, PENNSYLVANIA, DURING EARLY, MID AND LATE SEASON AUTUMN MIGRATION OF RED-TAILED HAWKS AT HAWK MOUNTAIN SANCTUARY, 1992–1994

	Period of autumn migration		
	Early[a]	Mid	Late
Hours of daylight[b]	11:57 ± 19.6	10:54 ± 18.6	9:56 ± 15.1
Mean daily temperatures (°C)	16.6 ± 1.63	10.8 ± 1.50	5.85 ± 1.60

[a] Early season = 14 Sept.–8 Oct.; Mid season = 9 Oct.–2 Nov.; late season 3–28 Nov.
[b] Hours of daylight and mean daily temperatures are from local climatological data monthly summary, Allentown, Pennsylvania. (NOAA 1992–1994).

weather patterns in the region (Miller 1976). Decreasing day length and solar azimuths combine to produce lower temperatures as the season progresses (Table 2), as well as fewer and less-powerful thermals relative to earlier in the season (Kerlinger 1989). In Pennsylvania, average daily temperatures drop 15°C between September ($\bar{x}$ = 17°C) and November ($\bar{x}$ = 2°C) (Cuff et al. 1989).

We have demonstrated that the extent to which Red-tailed Hawks respond to decreasing relative humidity declined over the migratory period, while their responses to wind direction and speed increased. Decreases in relative humidity, typically, are associated with the thermal-producing, fair-weather period that follows the passage of cold fronts at the site (Miller 1976). On the other hand, strong winds from the northwest produce ideal conditions for slope soaring along the southwest-to-northeast oriented ridge at Hawk Mountain (Brett 1991).

We believe seasonal differences in the way Red-tailed Hawks respond to environmental variables reflect a shift in migratory behavior from thermal to slope soaring, as conditions for the former decline during autumn, while those for the latter continue. A shift from thermal soaring to flapping flight in the second half of the autumn migratory season has been reported for the Levant Sparrowhawk (*Accipiter brevipes*) in Israel (Stark and Liechti 1993). The extent to which other species of raptors change their flight behavior over the course of autumn and spring migration remains an unexplored topic.

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MIGRATION OF THE WILLOW FLYCATCHER ALONG THE MIDDLE RIO GRANDE

WANG YONG[1] AND DEBORAH M. FINCH[1]

ABSTRACT.—We studied timing, abundance, subspecies composition, fat stores, stopover length, and habitat use of Willow Flycatchers (*Empidonax traillii*) during spring and fall stopover along the Middle Rio Grande, New Mexico. Spring migration started in mid-May and lasted about a month. Fall migration started in early-August and also lasted about a month. The most abundant subspecies was the Southwestern Willow Flycatcher (*E. t. extimus*), followed by *E. t. brewsteri*, *E. t. adastus*, and *E. t. traillii*. Nearly half of the Willow Flycatchers captured had no observable fat. Spring flycatchers had more fat stores than fall flycatchers. Willow habitat had the highest capture rate among the habitats sampled. Willow Flycatchers caught in willow habitat had higher fat stores than those caught elsewhere. Recaptured Willow Flycatchers had an average body mass gain of 1.6%/day with a short stopover length. Most Willow Flycatchers were unable to reach their destinations in a single flight, making it necessary for them to replenish their energy stores elsewhere en route. We suggest that the riparian woodlands of the middle Rio Grande provide important refueling sites for stopover flycatchers as they migrate between their breeding and wintering grounds.
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The Willow Flycatcher (*Empidonax traillii*) breeds extensively from southern British Columbia east to Maine and south to California, Arkansas, and Virginia. It winters in Middle America from Veracruz and Oaxaca south to Panama (A.O.U. 1983, USFWS 1995). The species prefers thickets, scrubby and brushy areas, open second growth, swamps, and open woodland, breeding primarily in swampy thickets, especially of willow and buttonbush (A.O.U. 1983). In the southwestern United States, populations of the species have declined through the 20th century (Hubbard 1987, Unitt 1987, USFWS 1995), primarily due to loss of riparian habitat, water development, cattle grazing, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and the invasion of riparian habitats by exotic tamarisk (*Tamarix* sp.) (USFWS 1995). The widespread reduction of riparian habitat essential for nesting and foraging is believed to have had the largest impact on the Willow Flycatcher's population (Remsen 1978, Harris et al. 1987, Unitt 1987). Owing to its severe population decline in the Southwest, the U.S. Fish and Wildlife Service listed the Southwestern Willow Flycatcher (*E. t. extimus*) as an endangered subspecies in 1995 (USFWS 1995).

This study provides basic information on migration biology, stopover

[1] USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 2205 Columbia SE, Albuquerque, New Mexico 87106.

ecology, and use of riparian habitats by Willow Flycatchers during spring and fall migrations along the Rio Grande in central New Mexico. Our objectives were to (1) document seasonal and daily stopover patterns, (2) examine energy (fat) stores, (3) determine fat redeposition rate and stopover length, (4) investigate use of different stopover habitats, and (5) document variations in stopover ecology among subspecies.

METHODS AND STUDY AREA

We established two study sites at the Rio Grande Nature Center (RGNC, 35°07′N, 106°41′W), Bernalillo County, and at the Bosque del Apache National Wildlife Refuge (BNWR, 33°48′N, 106°52′W), Socorro County, New Mexico. Field data were collected in spring from 4 April to 15 June 1994 and from 3 April to 9 June 1995 and in fall from 1 August to 13 November 1994 and from 31 July to 12 November 1995. *F*-tests from ANOVA of differences between sites and years were not significant for most variables, so we combined data collected in 1994 and 1995 across both sites for most analyses.

We used 20 standard, nylon mist nets (12 × 2.6 m) to capture Willow Flycatchers. The netting area was about 30 ha (net density ≈ 1.5 nets/ha) at each site. The nets were placed opportunistically at locations, such as brushy portions of wooded areas, forest edges or breaks, and near water, where birds could be captured most efficiently (Ralph et al. 1993). Unless rain, high winds, or temperature dictated a change, mist nets were opened 15 min before sunrise and operated approximately 6 h each banding morning. Each captured individual was weighed to the nearest 0.1 g using a digital electronic balance (ACCULAB V-333). Unflattened wing chord, tarsus, tail length, relative flight feather length (for wing formula calculation), presence of notch and emargination of the primaries, bill width, bill length, bill depth, lower mandible color, wing span, and tail shape were measured according to Svensson (1984) and Pyle el al. (1987). Skull ossification was examined in fall to identify age. Plumage color and relative contrast between parts of the body were recorded by referring to the color standards of Smithe (1975). Each Willow Flycatcher was banded with a numbered aluminum leg band.

We estimated fat stores of each Willow Flycatcher by observing the subcutaneous fat deposits in the interclavicular fossa and abdomen according to a six-point scale developed by Helms and Drury (1960). Estimates of body mass change during stopover were calculated as the difference in body mass between initial capture and last capture, and as the correlation between condition index (mass-wing^{-3}) and time of capture for all individuals captured (following Winker el al. 1992). The maximum potential flight ranges were estimated according to Pennycuick (1989) using a wing span of 210 mm (Yong and Finch, unpubl. data), energy density of 31 kj/g fat (Biebach 1992), still air, and air density of 1.23 kg-m^{-3}. Flight range estimates are valuable for generating migratory strategy predictions (Alerstam and Lindström 1990). Birds with zero observable fat could have internal fat detectable via lipid extraction analysis, so we estimated fat-free body mass by subtracting 3% (Berthold 1975) from the average body-mass of fat class zero birds.

Vegetation data from each net location were collected in 1995 based on a modified method of Daubenmire and Daubenmire (1968) and Daubenmire (1970). Habitats were characterized based on a riparian/wetland vegetation community classification developed by Durkin et al. (1996). We identified four major vegetation types: willow, agriculture field, cottonwood-Russian olive, and cottonwood-other vegetation.

The Willow Flycatcher has long been recognized for being geographically variable with four to five races recognized as valid (Phillips 1948, Phillips et al. 1964, Wetmore 1972,

Oberholser 1974, Hubbard 1987, Unitt 1987, Browning 1993). The breeding ranges of the widely distributed *E. t. traillii* and *E. t. campestris* extend across the northern United States and southern Canada, from New England and Nova Scotia west, through northern Wyoming and Montana, and into British Columbia. Hubbard (1987) and Unitt (1987) treated *E. t. campestris* as synonymous with *E. t. traillii*, but Browning (1993) considered them separate subspecies. The subspecies *E. t. adastus* breeds from Colorado west of the plains, west through the Great Basin States and into the eastern portions of California, Oregon and Washington. The breeding range of *E. t. brewsteri* extends from the central California coast north, through western Oregon and Washington to Vancouver Island. The breeding range of the Southwestern Willow Flycatcher, *E. t. extimus*, includes southern California, southern Nevada, southern Utah, Arizona, New Mexico, and western Texas (Hubbard 1987, Unitt 1987, Browning 1993, USFWS 1995).

These subspecies are distinguished primarily by subtle differences in color and morphology. In this study, we adopted the four-subspecies classification system of Hubbard (1987) and Unitt (1987). Subspecies identity using this system is based on measurements of wing, tail, wing formula (relative length of flight feathers), coloration of the head and neck and its contrast with the back, and the contrast between the breast-band and the throat (see Phillips 1948, Hubbard 1987, Unitt 1987, Browning 1993). Given morphological overlap and hybridization among subspecies, complete accuracy in identifying subspecies is not achievable.

All statistical analyses were performed with SPSS/PC + (SPSS 1994). Normality and homogeneity were examined prior to applying parametric tests, and nonparametric tests were used when these assumptions were violated. For sparse contingency tables we used Exact Test, a powerful method for obtaining accurate results when the data set is small (SPSS 1994).

RESULTS

For the two years combined, we operated 59,870 net-hours, and a total of 84 Willow Flycatchers (14 birds/10,000 net-h) were captured during spring (N = 42) and fall (N = 42) migrations. Spring passage started in mid-May, with first and last captures on May 13 and June 8, respectively. Fall migration started in mid-August with the first capture on August 9 and the last capture on September 16. The mean Julian capture dates of spring and fall migrations were day 148 (May 28) and day 241 (August 29), respectively. While spring migration peaked in the last week of May, no peak was observed in the fall based on weekly captures (Fig. 1). In fall, adults tended to migrate through earlier (Julian date 238 ± 11, $\bar{x}$ ± SD; N = 25) than hatching-year birds (Julian date 245 ± 11, N = 17, t = 1.96, P = 0.06). The daily timing of captures peaked around 08:00 (MST) in spring and around 09:00 in fall and the difference was not significant between seasons. About 70% of birds were captured between 07:00 and 09:00.

Fifty percent of the Willow Flycatchers captured did not have any observable subcutaneous fat stores (fat class 0) (Fig. 2), and only 11% had fat stores ranked at fat class two or higher. The average body mass was 12.7 ± 1.2 g with a range of 10.3 to 15.9 g. Body mass was signif-

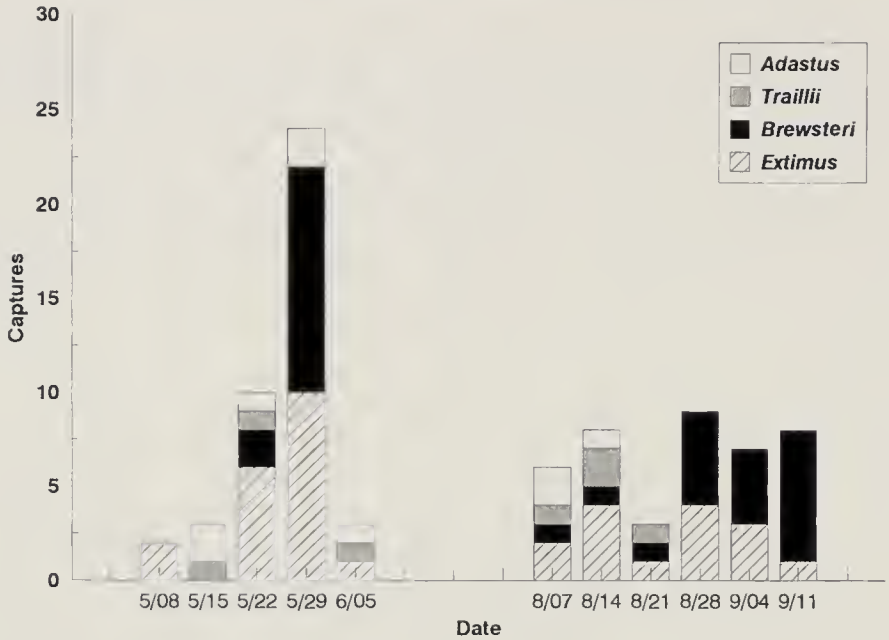

FIG. 1. Seasonal capture patterns of Willow Flycatcher (*Empidonax traillii*) during spring and fall migrations along the middle Rio Grande.

icantly different among fat classes ($F_{2,81}$ = 18.2, $P < 0.001$, Fig. 2). The average body mass of birds in fat class zero was 12.3 ± 0.9 g (N = 41). The estimated average fat-free mass of Willow Flycatchers was 11.9 g. Average body mass of flycatchers in fat classes one and ≥ two were 12.9 ± 1.1 g (N = 32) and 14.3 ± 0.75 g (N = 10), respectively. This translates to 1.0 g (8% fat-free body-mass) and 2.4 g (20% fat-free body-mass) fat stores, respectively. Average potential flight range was 225 km for all captures, 257 km for birds in fat class one, and 404 km for birds in fat class ≥ two (see Fig. 3 for depiction of relationship).

Body mass did not vary by capture date during spring and fall migrations. Wing length was negatively correlated with capture date in both spring and fall (Fig. 4a and 4b). Condition index increased during spring migration (r = 0.39, $P < 0.05$) but not during fall migration (Fig. 4c and 4d). Body mass of Willow Flycatchers captured in spring (13.2 ± 1.1 g, N = 41) was significantly higher (t = 14.42, $P < 0.01$) than that of the fall captures (12.3 ± 1.0 g, N = 42). The ANOVA test detected body mass differences ($F_{2,81}$ = 7.62, $P < 0.01$) among adult birds captured in spring (13.2 ± 1.1 g, N = 41), adult birds captured in fall (12.4 ± 1.2 g, N = 25), and hatching-year birds in fall (12.1 ± 0.8 g, N = 17). The multiple range tests suggested the difference was between spring birds and fall after-hatching year birds and between spring birds and fall hatching year birds (Tukey Test, $P < 0.05$). The difference between the two age groups in the fall was not significant.

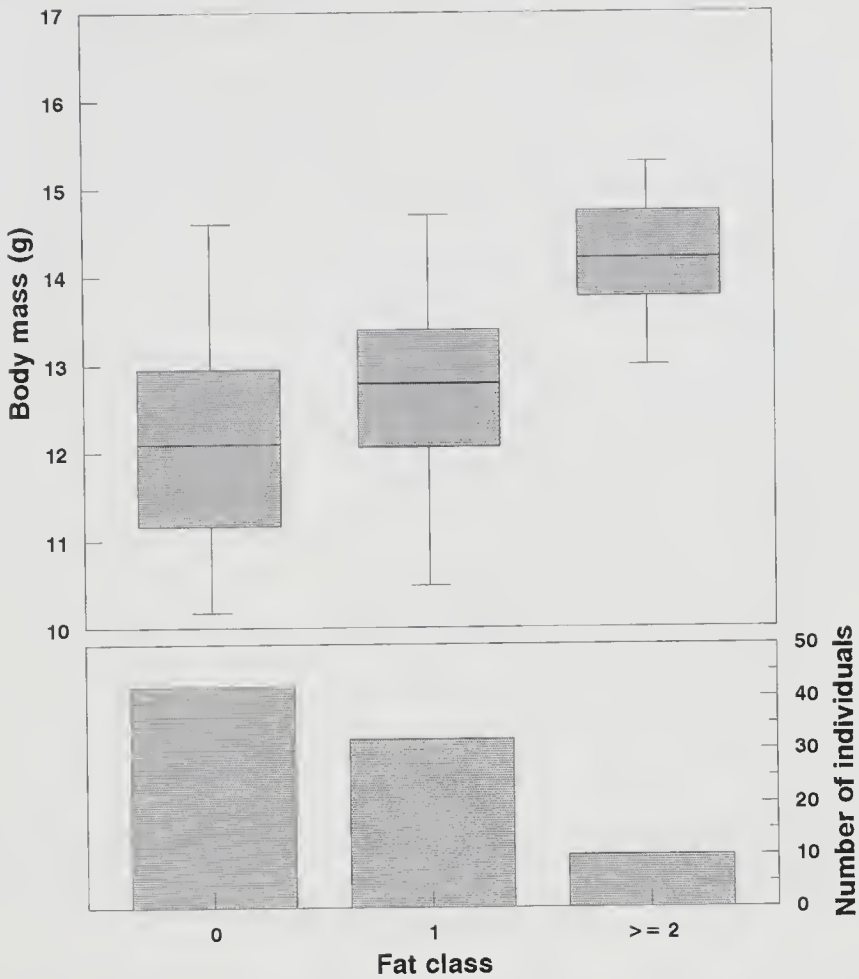

FIG. 2. Fat distribution and its relationship with body mass of Willow Flycatchers captured during spring and fall migrations along the middle Rio Grande.

Only seven Willow Flycatchers (8% total captures) were recaptured during the two-year field seasons. All recaptures occurred within one day after initial capture. Average body mass of recaptures was 12.4 ± 0.8 g at initial capture and was 12.6 ± 1.00 g at last capture, or an average change of 1.6% body mass/day. Body mass tended to be positively associated with daily time of capture in spring ($r = 0.28$, $P = 0.08$) and in fall ($r = 0.30$, $P < 0.05$). However, the partial correlation between daily time of capture and body mass, controlling for wing size variation, was not significant, suggesting that daily body mass change was due to the effect of smaller birds caught earlier in the day. Daily fat store accumulation estimates based on correlation between daily time of capture and condition index were not significant.

The capture rate of flycatchers among habitats deviated significantly from expected frequencies by net efforts ($\chi^2 = 30.67$, df = 3, $P < 0.001$, Table 1). Willow habitat had the highest capture rate (34.1 birds/10,000

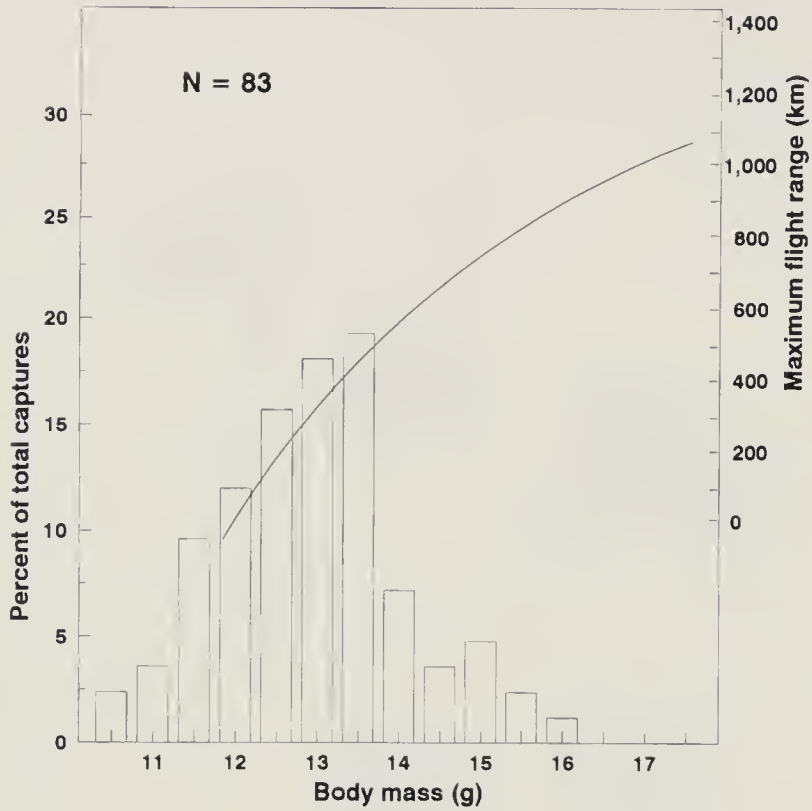

FIG. 3. Body mass distribution (bars) and maximum potential flight ranges (line) of Willow Flycatchers. The range estimations were based on the fat-free body mass of 11.9 g, wing span of 210 mm, still air, and air density of 1.23 kg-m^{-3}.

net-h), followed by cottonwood-Russian olive (16.0 birds/10,000 net-h), and agriculture (12.9 birds/10,000 net-h). The cottonwood-other habitat had the lowest capture rate (4.5 birds/10,000 net-h). The Exact Test suggested that the frequencies of occurrence of subspecies were independent of the frequencies of habitat type, suggesting that variation in habitat use was not subspecies related.

Body mass of flycatchers tended to be habitat dependent ($F_{3,80}$ = 2.26, P = 0.08): birds captured in willow habitat had the highest average body mass, while birds from agricultural fields had the lowest average body mass (Table 1). The amount of observable fat stores of birds captured from different habitats tended to be different (Kruskal-Wallis Test, χ^2 = 6.20, df = 3, P = 0.10), and the trend was perfectly correlated with the body mass variations among habitats (Spearman Correlation between average body mass and fat class of each habitat, r_s = 1.00, Table 1).

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FIG. 4. Seasonal changes of wing length and condition index (mass-wing^{-3}) of Willow Flycatchers captured during spring and fall migrations along the middle Rio Grande.

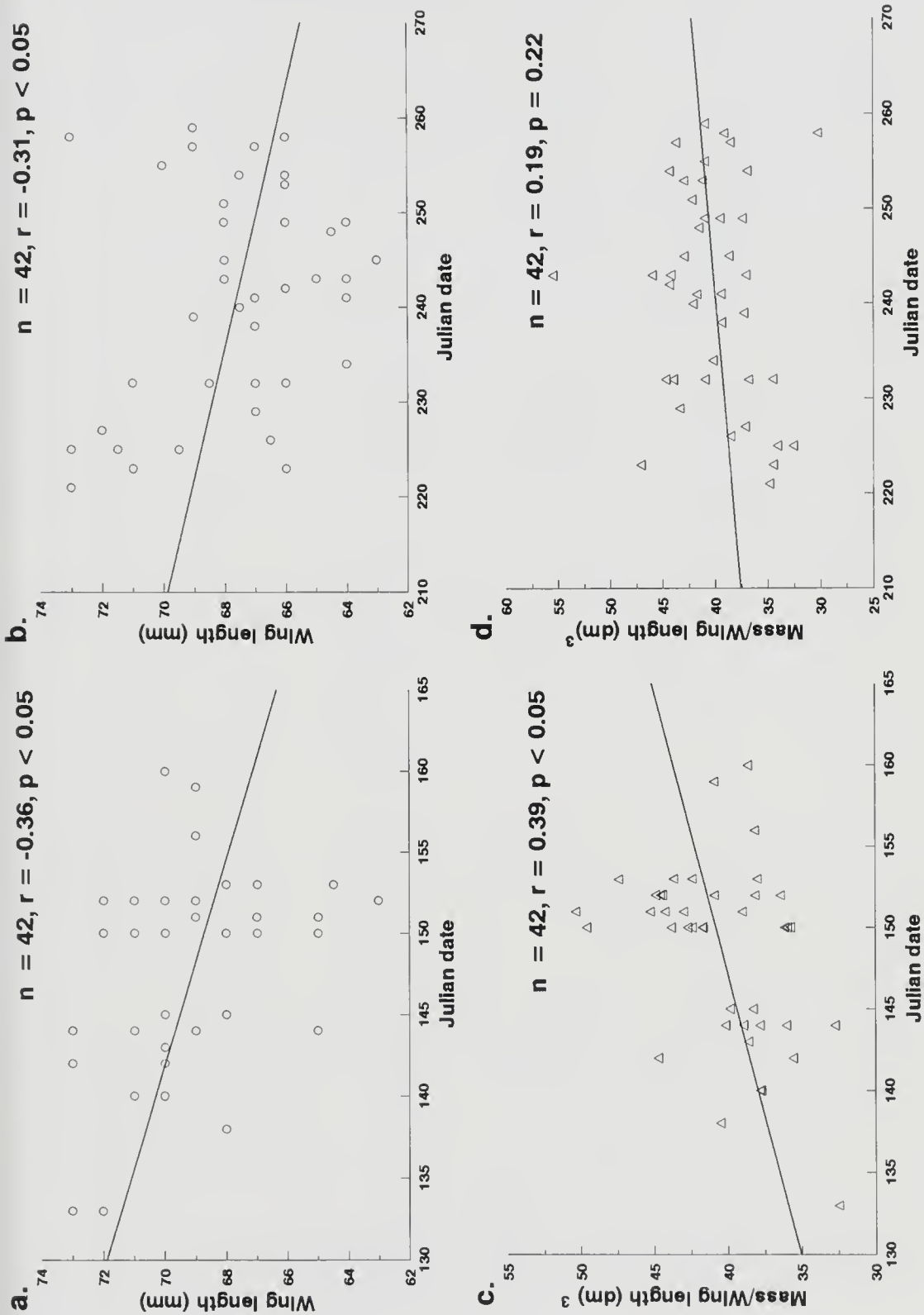
a.
n = 42, r = -0.36, p < 0.05
Wing length (mm)
Julian date
b.
n = 42, r = -0.31, p < 0.05
Wing length (mm)
Julian date
c.
n = 42, r = 0.39, p < 0.05
Mass/Wing length (dm) 3
Julian date
d.
n = 42, r = 0.19, p = 0.22
Mass/Wing length (dm)3
Julian date

TABLE 1

TOTAL NETTING HOURS, CAPTURE RATE (BIRDS/10,000 NET-H), BODY MASS, AND FAT CLASS OF WILLOW FLYCATCHERS

	Agriculture fields	Willow habitat	Cottonwood–Russian olive	Cottonwood–other vegetation	df	Statistic	*P*
Total netting hours	9336	6457	26,236	17,841			
Expected captures	13.1	9.1	36.8	25.0			
Actual captures	12	22	42	8	3	30.67[a]	<0.001
Capture rate	12.85	34.1	16.00	4.5			
Body mass (g)[d]	12.09 ± 0.94	13.12 ± 1.19	12.69 ± 1.18	12.91 ± 0.95	3,79	2.26[b]	0.08
Fat class[d]	0.42 ± 0.51	0.95 ± 0.84	0.55 ± 0.80	0.75 ± 0.71	3	6.20[c]	0.10

[a] Goodness-of-Fit (χ^2).
[b] One-Way ANOVA (*F*).
[c] Kruskal-Wallis One-Way ANOVA (χ^2).
[d] Mean ± SD.

Of the 84 Willow Flycatchers we sampled, the Southwestern Willow Flycatcher (*E. t. extimus*) was the most abundant subspecies (N = 34), followed by *E. t. brewsteri* (N = 33), *E. t. adastus* (N = 9), and *E. t. traillii* (N = 7). One individual was not identified. Average capture dates differed among subspecies during fall migration ($F_{3,37} = 7.51$, $P < 0.001$, Table 2) but not in spring. The multiple comparisons suggested that *E. t. brewsteri was* significantly later than the other three subspecies in fall (Table 2). Mean capture dates between the earliest subspecies, *E. t. traillii*, and the latest subspecies, *E. t. brewsteri*, differed by only three days in the spring, while the difference between the earliest subspecies, *E. t. adastus*, and the latest subspecies, *E. t. brewsteri*, in fall was 24 days. The endangered Southwestern Willow Flycatcher migrated through the area between May 13 and June 8 (May 28 ± 6.8 days, N = 19) in spring and between August 13 and September 11 (August 27 ± 9.8 days, N = 15) in fall. Subspecies moving through the study sites earlier in spring tended to migrate back earlier in the fall (Spearman Correlation between average spring julian capture date and average fall julian capture data, $r_s = 0.80$).

Wing length, tail length, and tarsus significantly varied among the four subspecies (Table 2). The multiple comparisons suggested that tarsus length of *E. t. traillii* was significant longer than that of *E. t. brewsteri* and *E. t. extimus*, that wing length of *E. t. brewsteri* was significantly shorter than *E. t. traillii* and *E. t. adastus*, and that tail length of *E. t. brewsteri* was significantly shorter than that of *E. t. extimus*. Body mass and fat stores did not vary among the four subspecies.

DISCUSSION

Based on records from New Mexico, Hubbard (1987) suggested that "the extreme dates of occurrence of Willow Flycatchers in New Mexico are May 1 to September 16" and that "spring migration persists into early June, and autumn migration begins in late July. Our data confirm that Willow Flycatcher migration occurs in late spring and early fall. The duration of migration passage was only about one month each in spring and fall. Rosenberg et al. (1991) suggested that low-elevation breeding populations, all thought to be *E. t. extimus*, migrated early, arriving on their breeding grounds in late April and early May, whereas montane-breeding populations, such as *E. t. brewsteri* and *E. t. adastus*, arrived in mid-May and continued to pass through the lower Colorado River valley into mid-June. Unitt (1987) also indicated that spring migration of *E. t. extimus* was earlier than that of *E. t. brewsteri*. Mean capture dates during spring migration along the middle Rio Grande did not statistically differ among subspecies. Similarly, Suckling et al. (1992) reported no strong differentiation among subspecies spring arrival dates on the breeding

TABLE 2

MORPHOLOGICAL MEASUREMENTS AND CAPTURE DATE ($\bar{x}$ ± SD) OF SUBSPECIES OF THE WILLOW FLYCATCHERS

	Subspecies					
	adastus	*brewsteri*	*extimus*	*traillii*	df	*F*
N	9	33	34	7		
Mass (g)	13.31 ± 1.19	12.59 ± 1.13	12.73 ± 1.16	13.07 ± 0.84	3,78	1.27
Wing length (mm)	70.67 ± 2.12	67.29 ± 2.70	68.46 ± 2.44	70.00 ± 2.24	3,79	5.55**
Tail length (mm)	58.00 ± 1.58	56.15 ± 2.97	57.82 ± 2.38	58.29 ± 2.81	3,79	3.11*
Tarsus (mm)	16.53 ± 0.78	16.52 ± 0.71	16.79 ± 1.00	17.73 ± 1.80	3,79	3.19*
Fat class	0.78 ± 0.44	0.82 ± 0.92	0.59 ± 0.74	0.14 ± 0.38	3	5.63[a]
Spring capture date[b]	146.83 ± 8.35	149.86 ± 2.82	147.68 ± 6.76	146.67 ± 8.33	3,38	0.55
Fall capture date	223.67 ± 3.06	247.42 ± 10.39	238.93 ± 9.79	232.00 ± 5.72	3,37	7.51***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[a] Kruskal-Wallis One-Way ANOVA.

[b] = Julian date.

grounds. Difference in timing of fall passage was more obvious among subspecies in our study: the Pacific subspecies, *E. t. brewsteri* migrated through the study sites latest, while the Southwestern Willow Flycatcher had a relatively broad passage period.

Wing length, tail length, and tarsus varied among subspecies. In contrast, body mass did not vary by subspecies but did differ between seasons. In many passerine species, wing length and body size vary in relation to age and sex (Pyle et al. 1987). We speculated that flycatcher body mass may have been significantly lower in fall than in spring if hatching-year birds weighed less than adults. Although body mass of young fall birds significantly differed from that of spring adults, it did not differ from fall adults. Therefore age only partially explained body mass variation between spring and fall.

Body mass did not vary within each migration season, but declines in wing length through spring and fall and increases in condition index through spring suggest that flycatcher condition and wing size may be related to departure times (and travel distances) of different groups of flycatchers. Spring capture dates did not vary by subspecies (although fall capture dates did), so subspecies alone does not explain within-season variation in condition and wing length. Such variation may be related to sex or age, or interactions of sex with age or subspecies. Interpretation of other breeding studies suggests that arrival and departure times of Willow Flycatchers vary in relation to sex and age, and consequently such factors are likely to contribute to changes in mass within and between migration periods. For example, male Willow Flycatchers are reported to arrive on the breeding grounds ahead of females, based on behavioral observations (Bent 1942, Walkinshaw 1966). Males of other passerine species are also reported to migrate before females (e.g., Francis and Cooke 1986, Morton 1992), possibly due to competition among males for high-quality territories, ability to tolerate harsher weather than females, and differences between males and females in travel distances to breeding and wintering areas. Thus, some of the changes in body condition and wing length that we detected during spring and fall migrations may be related to variation in departure times of sexes, with males leaving before females in both seasons. In spring, females may prepare in advance for the high energy costs of egg-laying by depositing more fat in proportion to wing length than males.

In addition to differences in departure time between sexes and among subspecies in fall, adult Willow Flycatchers are reported to head south earlier than hatching-year birds (Unitt 1987), thus further complicating interpretation of intra-seasonal changes in body size and condition during migration. Adult Willow Flycatchers can start migrating earlier in fall

than young birds because they delay molting (postnuptial or prebasic) until they reach their wintering ground in Central and South America. By contrast, young flycatchers molt into their first winter (basic) plumage prior to migration, which adds to the length of their stay on the breeding grounds (Unitt 1987, Hubbard 1987). Our results showed that hatching-year birds tended to migrate through the Rio Grande valley later than adults, suggesting that age-related departure time may be a complicating factor in explaining seasonal decreases in wing length in fall. Interaction effects of age with subspecies and sex may have masked fall variation in attributes such as body mass and condition between adults and hatching-year birds.

In anticipation of the high energy demand of migration, small landbird migrants deposit fat stores before their long-distance flight. Nonmigratory birds have lipid contents of only 3–5% of lean body mass, whereas migratory birds can deposit fat stores of up to 30–50% of lean body mass (Berthold 1975). However, small landbird migrants, especially Neotropical long-distance migrants, generally do not deposit enough fat to fly nonstop between breeding and wintering grounds. In this study, about 50% of the Willow Flycatchers had no fat stores, which is lower than that reported for other species (e.g., Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Winker et al. 1992, Yong 1993).

Low fat stores in Willow Flycatchers could be caused by depletion of fat stores during nocturnal migration. Moore and Kerlinger (1987) found that arrival condition, as indexed by amount of fat stores, of trans-Gulf migrants was significantly related to wind direction and precipitation. Alerstam and Lindström (1990) proposed that low fat stores in stopover migrants could be a behavioral response to minimize energy needed for migration: lighter birds keep flight costs lower than heavier birds by storing only enough fat to reach the next stopover site. Maintaining a low body mass could also help to reduce the energetic cost of foraging during stopover, especially in wing-foragers such as the Willow Flycatcher. In any case, owing to low fat stores, Willow Flycatchers are seemingly constrained to feed at stopover sites such as our study area to make progress toward their breeding or wintering destination.

The condition index estimates failed to show daily increases in body mass during stopover. Although our analysis of recapture data was hampered by relatively small sample size, recaptured Willow Flycatchers had higher average body mass, which suggests increase of fat stores during stopover. Additional data are required to confirm this pattern. Rate of body mass gain (1.6% of initial body mass) of the Willow Flycatchers is similar to estimates for other species (Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Winker et al. 1992). Based

on the results of low recapture rate and short duration between capture and recapture (birds were recaptured only within one day after initial capture), we conclude that stopover length of Willow Flycatchers at our study sites was relatively brief. Proportional gain of body mass and short stopover length suggest that Willow Flycatchers were able to find food quickly and efficiently in stopover habitats to redeposit energy stores for migration.

Previous research has shown that landbird migrants use specific habitats and select among alternative vegetation types during stopover (e.g., Bairlein 1983, Moore et al. 1990, Winker et al. 1992, Mabey et al. 1992), presumably in response to differential suitability among habitats (Hutto 1985, Moore and Simons 1992). We evaluated whether variation in capture rates among mist-nets was related to kinds of habitats that nets were erected in. Mist-net locations that had relatively high captures of Willow Flycatchers in our study were characterized by a relatively open overstory and dense mid-/and low-stories, close proximity to water, and presence of willows or Russian olives. Net sites in willow captured the greatest proportion of stopover Willow Flycatchers, followed by net sites in dense young cottonwood-Russian olive stands. In addition to plant species composition, vegetation structure may influence capture rates (Remsen and Good 1996), i.e., flycatchers may be captured more frequently in habitats with dense shrub vegetation than in open, shrubless habitats (e.g., cottonwood-other or agriculture), regardless of cottonwood presence or absence. Hirsch and Segelquist (1978) found that Willow Flycatcher numbers were positively correlated with willow volume during breeding season.

During this study, we observed Willow Flycatchers actively foraging within dense willow habitat, taking insects on the wing and gleaning from foliage. Densities of arthropods are high in willows relative to other vegetation (Yong and Finch, unpubl. data). We hypothesize that migrating Willow Flycatchers stop more frequently in willow habitats than in other habitat types because willows contain more arthropod food that flycatchers favor. We recommend that this hypothesis be tested through experimental manipulations of food supply, habitat, and flycatcher foraging behavior in willow versus other habitat types. For example, arthropods could be experimentally removed from individual willows and other plant species by fogging with a stunning solution, then observers could monitor flycatcher foraging responses to fogged and unfogged plants.

Up until now research and conservation efforts pertaining to the Willow Flycatcher have focused on its breeding grounds. The energetic consequences of flycatcher migration and the need for suitable en route habitat for refueling are largely overlooked as factors affecting the survival of adult and hatching-year Willow Flycatchers. Our results, however, suggest

that riparian woodlands along the middle Rio Grande are important as stopover sites for resting and fat redeposition by the Willow Flycatcher during its spring and fall migrations. If migrating Willow Flycatchers cannot periodically replenish their fat stores and do so quickly, the probability of a successful migration is reduced. We recommend that flycatcher stopover habitats, especially native shrubs such as coyote willow, be actively monitored, maintained, and preserved to protect endangered Southwestern Willow Flycatchers.

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NORTHERN CARDINAL SEXES DEFEND NESTS EQUALLY

PAUL M. NEALEN[1,2] AND RANDALL BREITWISCH[1]

ABSTRACT.—We exposed nesting Northern Cardinals (*C. cardinalis*) to models of three predators of cardinal eggs or nestlings (black rat snake [*Elaphe obsoleta*], Blue Jay [*Cyanocitta cristata*], and eastern chipmunk [*Tamias striatus*]). We attempted to determine relative contributions to nest defense by males and females during the mid-nestling stage of the nesting cycle. For all defense variables monitored, mean responses did not differ between the sexes, although females spent more time in attendance at the nest. Latency to response to the models was strongly correlated between mates, but responses by mates appeared to be independent at the nest. There was little evidence for stimulus-specific defense. Parent bird responses to the predator models and to a mounted Mourning Dove (*Zenaida macroura*, a "non-threat") likewise did not differ. Active defense of nests may be of limited importance to reproductive success in this cardinal population. *Received 7 May 1996, accepted 20 Oct. 1996.*

Mates of biparental species invest considerable time and energy in the production of independent offspring (Clutton-Brock 1991). However, studies of parental care in many passerines suggest that male and female parental roles can differ; the sexes may contribute disproportionately to brooding, nestling feeding, or to other components of care, including nest defense (e.g., Breitwisch 1988, Rytkönen et al. 1993). Theoretically, individuals of both sexes act to maximize their own reproductive success (Trivers 1972). Such a strategy can produce apparently cooperative behavior between mates, as males and females invest in the same offspring. However, individuals need not invest equally, despite the shared benefit of offspring production (e.g., Maynard-Smith 1977).

The sexes may be predicted to differ in their parental effort if their costs and benefits of that effort are unequal (Montgomerie and Weatherhead 1988). For example, male-biased operational sex ratios (as often found in passerines; see Breitwisch 1989) may lead to unequal levels of care between the sexes (Trivers 1972, Breitwisch et al. 1986). Further, individual characteristics (e.g., age, experience, body condition, certainty of parentage) may differ within pairs, causing mates to differ in their ability or willingness to engage in parental care (Redondo 1989). Additionally, males and females of dichromatic species may face very different risks in engaging in some aspects of parental care. The presence of the more "visible" sex at or near the nest may increase the probability of

[1] Biology Dept., Univ. of Dayton, Dayton, Ohio 45469-2320.
[2] Present address: Biology Dept., Univ. of Pennsylvania, Philadelphia, Pennsylvania 19104-6108.

attraction of a visually-orienting predator dangerous to the nest contents or the adult bird (Skutch 1976).

The Northern Cardinal (*C. cardinalis*) is a monogamous and biparental passerine which builds open-cup nests within several meters of the ground (e.g., Kinser 1973). Cardinals are highly dichromatic, males having brilliant red plumage, while females have brown plumage. In our study population, the rate of nest predation was severe, and little influenced by nest location (Filliater et al. 1994). Thus, parental defense of nest contents may be crucial for reproductive success in this population. Given the potential for males and females to differ in their levels of activity around the nest because of inequalities in the costs and benefits of doing so, we investigated the relative contributions of the sexes to the active defense of their nests. Our primary goal was to examine sex differences in defensive behavior, an important component of avian parental care (Montgomerie and Weatherhead 1988).

STUDY AREA AND METHODS

We conducted this study in 1992 and 1993 at the Aullwood Audubon Center and Farm, a National Audubon Society property ca. 15 km NW of Dayton, Ohio (see Filliater et al. 1994 for site description). Defense levels were measured for 24 breeding pairs by presentation of a predator model at the nest during the mid-nestling stage (nestlings aged 3-8 days post-hatch). At this stage in the breeding cycle, both sexes visit the nest with or without food for the nestlings (pers. ob.); females brooded nestlings periodically as well. Each pair was exposed to only one of three different predator models [taxidermic mounts of an Eastern Chipmunk (*Tamias striatus*) and Blue Jay (*Cyanocitta cristata*), and a black rubber snake ca 1.2 m in length colored to resemble a black rat snake (*Elaphe obsoleta*)]. The response of each pair to a taxidermic mount of a Mourning Dove (*Zenaida macroura*, a "non-threat") was also measured. In 1992, experimental trials were conducted with 18 different breeding pairs. Each of the three predator models was used at six different nests. In 1993, six additional trials were conducted with the snake model to which was attached a monofilament line. This was used to move the head of the snake model slightly, ca once per minute while in place at the nest (e.g., Siderius 1993, Maloney and McLean 1995). Each pair tested in 1993 was exposed to the stationary dove model as before.

All experimental trials were begun between 06:00–09:30 EST. Two persons were involved in each trial. One person handled the models and then withdrew from the immediate area. The second individual remained stationary on the ground, behind vegetation if possible, and recorded observations from a distance of 10–12 m from the nest. Before model presentation, parental nest visits were monitored (average duration 84 min) to ensure that both parents were attending the nest. Once both parents were out of view, the first model was placed at nest height, ca 1 m from and facing the nest. The model was placed so that it appeared to be resting on a limb or twig. The use of the dove or predator model first was alternated between trials.

The duration between model placement and parent bird return averaged 9 min (range: 1–33 min). Once either or both parent birds returned to within 10 m of the nest, data were collected for 3 min. Observations of parent bird defensive response and location relative to the nest and model were spoken into a tape recorder and were collected separately for mates if both responded. After 3 min, the handler approached and removed the model. Undisturbed

(no model in place) nest visits were again monitored, for an average of 105 min (range: 86–178 min). After this period, the second model (either dove or predator) was placed as before. Again, one or both parent birds returned after a short duration ($\bar{x}$ = 13 min), and their response was monitored for 3 min. Once the second model was removed, post-trial nest visits were then monitored ($\bar{x}$ = 35 min).

The first variable monitored was the duration between model placement and parent bird return to within 10 m of the nest (response time: RT). Because parent birds did not always feed the nestlings when visiting the nest, we took RT as a measure of the latency for parent bird discovery and response (e.g., Curio and Regelmann 1987). We also measured the portion of the 3-min response period for which a bird remained within 10 m of the nest (time present: TP). Parent bird distance to the model was estimated and recorded each time a bird changed its location; from these data parent bird closest (CDM) and furthest distance to the model (FDM) were determined. Parent bird distance to the model at the end of each 15 sec interval during the 3-min response period was also noted; these interval-end distances were averaged to provide mean distance to the model (MDM).

Parent bird calling rate (CR, calls/min) was also determined. Only one type of call (variously described as "chip" or "click") was counted. These calls are known to be used in situations of agonism or alarm (Lemon 1968, Kinser 1973) and made up the vast majority of cardinal vocalizations during nest visits (PMN, unpubl. data). In addition, any threat displays or attacks on the model were noted.

Many nests visits by both sexes before, between, and after model presentations were observed. Visit frequency, mean duration, and calls/visit were tabulated for both sexes to allow an assessment of overall nest attendance and call usage during these undisturbed (no model present) nest visits. Brood characteristics (size and age) were also recorded to determine the cues by which the sexes may determine their defense levels.

A total of 24 pairs of birds was sampled. However, responses by only one member of a pair were common. Likewise, some birds made no nest visits between or after model presentations. As such, sample size varies among analyses. To simplify presentation, for some analyses a single value N_t is given to reflect the total number of individuals sampled (up to a maximum of 24 of each sex) in an incomplete block design (Sokal and Rohlf 1981, p. 394).

Nonparametric statistical tests (Siegel and Castellan 1988, SAS Institute 1990) were employed. Paired analyses were used when possible (e.g., mates within pairs or a bird acting as its own control). However, the frequent lack of response by one member of a pair necessitated the use of non-paired analyses in some cases.

Variable means were compared by the Wilcoxon matched-pairs, signed ranks test (T value reported) for paired comparisons and by the Mann-Whitney U-test (U value reported) for $k = 2$ independent cases. Variable mean comparisons for $k > 2$ independent cases were by the Kruskal-Wallis one-way ANOVA (H value reported). The G-test (G_{adj} reported) or binomial test was used to measure association; Spearman rank correlations (r_s reported) were used to examine the strength of variable correlations.

All tests were two-tailed unless otherwise stated. The α value for significance of statistical tests was set at $P = 0.05$ for singular comparisons. The comparison-wise error rate (Chandler 1995) was conservatively reduced to α/k for k simultaneous comparisons.

RESULTS

Response to models.—An assumption of this experiment was that the parent birds responded to the presence of the models near their nest. This was tested by comparing the number of calls given by parent birds on

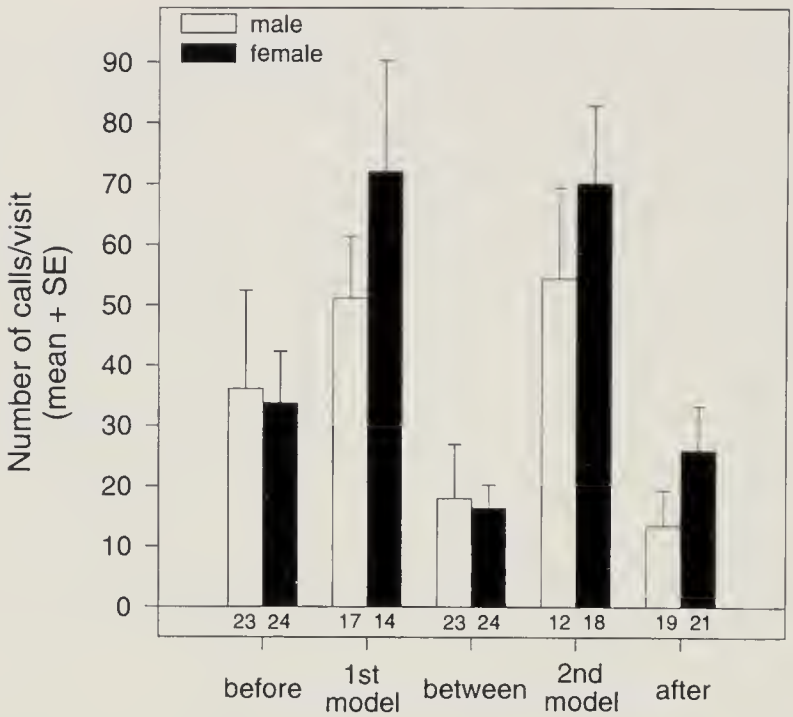

FIG. 1. Grand mean + SE of the number of "chip" calls given on nest visits by Northern Cardinals before, between, after, and during model presentations. Number of birds sampled given below bars.

visits to the nest when *any* of the models was present with the number of calls given on nest visits before, between, and after model presentations (visits during which females brooded nestlings were excluded).

Males gave similar numbers of calls on nest visits before, between, and after model presentations (H = 2.12, N_t = 23, df = 2, NS) as did females (H = 3.38, N_t = 24, df = 2, NS; Fig. 1). Males gave similar numbers of calls to the first and second models (U = 89.5, N_t = 16, NS) as did females (U = 124.0, N_t = 18, NS). However, more calls were given during model presentations than when no model was present both by males (T = 11.0, N = 18, P = 0.0013) and by females (T = 23.0, N = 23, P = 0.0014). Both sexes called at higher rates during nest visits when models were in place (males, T = 43.0, N = 19, P = 0.04; females, T = 53.0, N = 21, P = 0.03). In addition, nest visit mean duration was greater, when models were in place, for both males (T = 24.0, N = 19, $P < 0.005$) and females (T = 28.0, N = 21, P = 0.0025). These results suggest that parent birds clearly responded to the presence of the models, but that encountering a model at the nest had no apparent lasting effect on the birds' behavior.

Our planned comparisons were to examine male-female response differences. Because several predator models were used to elicit defensive behavior, we first examined within-sex defensive behavior among the

predator model types for each of the response variables monitored (for example, male response time was compared among the different predator model types). For both males (H = 1.03 to 4.97, N_t = 17, df = 3, all NS) and females (H = 2.33 to 8.53, N_t = 16, df = 3, all NS), no model-specific behaviors were detected. This suggests that response data may reasonably be pooled among the predator models for each sex.

We then compared responses to the predator versus the dove models for each sex. The strongest inference of predator-dove model response differences is obtained from paired data of individuals which responded to both models (for example, comparison of individual male response times to the dove and predator models). For all variables, the responses given by males (T = 10.0 to 20.0, N = 9, all NS) and females (T = 5.0 to 30.0, N = 11, all NS) to the control and predator models did not differ. A total of 12 males and 16 females responded to the dove model; a total of 17 males and 16 females responded to the predator models. Unpaired analyses (which make use of all available data) of all defense variables monitored likewise suggest no difference in response to the dove or predator models for either sex (males, U = 74.5 to 97.5, all NS; females, U = 89.5 to 122.0, all NS).

Male-female responses.—For those pairs which responded in tandem to the predator models, male and female responses did not differ for any of the response variables monitored (T = 6 to 17, N = 9, all NS). Only response time to the predator models was correlated between mates (r_s = 0.96, N = 9, $P < 0.01$). Nonpaired analyses were used to examine the full set of response data available (responses from 20 males and 21 females; as no differences in response between the dove and predator models were found, response data were pooled by individual). Again, for each of the defense variables measured, no differences between male and female responses were found (U = 133 to 206, all NS).

Both mates in a pair responded during four of 24 dove model presentations and nine of 24 predator model presentations (binomial test, NS). We found no association between model type (dove or threat) and the frequency of response by the sexes (G_{adj} = 0.10, df = 1, NS) or between model type and the sex of the first-arriving bird (G_{adj} = 0.12, df = 1, NS; Table 1).

No birds made contact with the snake model. However, the snake model elicited "fluff-out" (threat) displays (see Lemon 1968, Kinser 1973) from one of nine responding males and one of nine responding females (not mates), a distinctive "chitter" call (described in Lemon [1968] as a mark of agonism) from three males and two females, and one mixed-species mobbing. The jay model was struck bodily by one of four responding males and one of three responding females (not mates). One of

TABLE 1
MALE AND FEMALE RESPONSE PHENOLOGY TO DOVE AND PREDATOR MODELS[a]

Model	F alone	F first, then M	F = M	M first, then F	M alone
Dove	12	1	2	1	8
Predator	7	4	2	3	8

[a] Given are the number of model presentations which followed each pattern of parent bird response sequences.

16 responding females struck the dove model. No birds attacked or displayed at the chipmunk model.

Brood characteristics and defense.—Modal brood size in this population was two (Filliater and Breitwisch 1997), which represents the brood size of 12 of the 24 pairs tested here. The duration of female response (Time Present) was the only aspect of either male or female defense which was strongly correlated with brood size ($r_s = 0.64$, $N = 16$, $P < 0.01$). Male closest (CDM: $r_s = -0.57$, $N = 17$, $P < 0.025$) and mean (MDM: $r_s = -0.59$, $N = 17$, $P < 0.025$) distances to the models were negatively correlated with brood age. No measure of female defense was correlated with brood age.

The relationship between defense and the subsequent success of the nest (in terms of the number of young fledged) was also examined for each sex. FDM values during model presentations were strongly and negatively related to the subsequent success of that nest; i.e., females which stayed close to the nests during model presentations produced more young ($r_s = -0.63$, $N = 16$, $0.005 < P < 0.01$, 1-tailed test). No measure of male defensive response was strongly correlated with this measure of nest success ($r_s = -0.45$ to 0.36, $N = 17$, all NS).

Nest attendance.—A total of 506 nest visits over nearly 100 h of observation on these 24 pairs of birds was logged. Data for one male were excluded as he made no trips to the nest despite being nearby. Males and females made similar numbers of visits ($T = 69.0$, $N = 20$, NS), but visit duration was much greater for females than for males ($T = 41.0$, $N = 23$, $P < 0.005$). As such, overall attendance (proportion of observation time spent at the nest) was greater for females than for males ($T = 59.0$, $N = 23$, $P < 0.025$).

DISCUSSION

While the use of model predators to elicit avian parental defensive responses has been criticized as being artificial or inappropriate (e.g., Knight and Temple 1986), models are advantageous for a number of reasons. Living predators may provide an inconsistent stimulus, due either

to their being restrained or for physiological (e.g., Hamerstrom 1957) or other reasons, and can be very difficult to present efficiently (D. Winkler, pers. comm.). Alternatively, stuffed mounts can be presented in a consistent fashion and have been used extensively (e.g., Knight and Temple 1988, Neudorf and Sealy 1992, Rytkönen et al. 1993, Maloney and McLean 1995). Given that parental nest visitation behavior was noticeably affected by the presence of models at the nest, we feel justified in concluding that parent birds did indeed respond to the models, be they recognized merely as "intruders", or more specifically by type (e.g., "avian intruder" versus mammal or snake), or by species.

Cardinal defensive responses.—Parent birds responded similarly to *all* of the models presented. This is a rather unexpected finding, given that a number of passerines have previously been shown to tailor their defensive response to the apparent threat posed by different stimuli (e.g., Buitron 1983, Curio et al. 1983, Knight and Temple 1988) and to exhibit rapid, learned predator recognition (Maloney and McLean 1995). However, only the avian models (jay and dove) were struck, and only the snake model elicited threat displays and a group mobbing. This suggests that the models may have been perceived as being different and highlights the difficulty of comparing the "intensity" of different types of behaviors.

Previous studies of sex-differences in nest defense by other passerines (including the Northern Mockingbird [*Mimus polyglottos*; Breitwisch 1988] and Red-winged Blackbird [*Agelaius phoeniceus*; Knight and Temple 1988]) have demonstrated marked differences in male and female defensive behavior. However, by all measures of active defense monitored, males and females in this population appear to contribute equally to the defense of their nest during the mid-nestling stage. Although larger sample sizes might have helped to clarify male and female roles in providing defense, the lack of sex differences reported here is not simply a function of our effort, as marked sex differences in nest defense by other passerines have been demonstrated in studies employing similar methodologies and sample sizes (e.g., Breitwisch 1988, Knight and Temple 1988, Curio and Onnebrink 1995). Sex differences in nest defense may best be detected in species which provide intense defense; cardinal nest defenses generally appear to be of low intensity but are highly variable. In general, no model was ignored (including the dove model): parent birds increased their call rate and number of calls and lengthened visit duration when models were in place at the nests (see Results). However, no model consistently elicited intense responses from either sex.

Females exhibited greater nest attendance than did males, at least in part due to female brooding of young. Greater attendance by one sex is of consequence if the sex with higher nest attendance is more likely to

(at least initially) encounter and respond to an approaching threat to the nest contents. Responses by single birds were common but were not biased toward females. This suggests that the sexes may have equal probability of discovering a threat that arrives at the nest during parental absence. Once at the nest, mates' responses were generally independent; there was little indication that defensive behavior might be "matched" between mates, as suggested by Breitwisch (1988) for Northern Mockingbirds; nor was there evidence for differential parental effort by mates as suggested by Burley (1986) for sexually-selected species.

Our study was designed to use each member of a pair as a control for its mate, in order to account for differences among pairs in factors which may influence defense levels, such as brood size or age (see review in Montgomerie and Weatherhead 1988). The efficacy of this experimental design was weakened when both mates did not respond and non-paired analyses were necessary. However, the importance of brood size as a determinant of nest defense intensity is not always demonstrable (e.g., Hogstad 1993, Rytkönen et al. 1995, Curio and Onnebrink 1995). Monogamous mates invest in a single brood of some size and age, but it remains possible for mates to respond to different cues relating to the brood (e.g., size versus age). The power of our tests of the influence of brood size and age is somewhat limited by the number of comparisons made, but the data suggest that males and females may indeed perceive or respond to different cues relating to brood characteristics.

Importance of defense.—Our results suggest that active defense played a relatively minor role in influencing nest success in this cardinal population. Although adults struck the predator models on several occasions, most defense was of much lower intensity (e.g., calls, some movements around nest area). Parent birds may have little ability to deter threats to their nests without assuming unacceptably high risk to themselves; this may be especially true of snakes, which are important predators of young birds (Skutch 1976, pers. ob.). Annual reproductive success in this population has been estimated at 15%, with predation as nearly the sole cause of nest losses (Filliater et al. 1994), but cardinals appear not to defend vigorously their current investment in a brood. Rather, reproductive success is achieved by rapidly renesting if the current clutch or brood is lost. Scott et al. (1987) have shown that cardinals can begin laying a new clutch in as few as four days ($\bar{x}$ = 5.5 days) after nest failure and have relatively long breeding seasons. We have witnessed such rapid and repeated renestings in this population; individual pairs attempted six or more nests in a single season lasting ca. 130 days (PMN, unpubl. data). In this population, renesting may be a better option than intense defense of the current brood.

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THE CONTEXT AND FUNCTION OF DUET AND SOLO SONGS IN THE RED-SHOULDERED BLACKBIRD

LINDA A. WHITTINGHAM,[1,2] ARTURO KIRKCONNELL,[3] AND LAURENE M. RATCLIFFE[1]

ABSTRACT.—We examined the social and behavioral context of male and female duet and solo songs in Red-shouldered Blackbirds (*Agelaius assimilis*), formerly known as the Cuban race of the Red-winged Blackbird (*A. phoeniceus*). Songs were most common during intersexual interactions before birds were on breeding territories. In contrast to Red-winged Blackbirds, Red-shouldered Blackbirds sang relatively little and aggressive interactions were rare when they were on breeding territories. Our results suggest that duet and solo songs are important in pair bond formation and maintaining contact between mates. *Received 28 May 1996, accepted 15 Oct. 1996.*

The function of song has been studied in many species; however, studies have focused primarily on the function of male song. The study of female song has been restricted mostly to tropical species in which females sing frequently, usually in the form of a duet with her mate (Farabaugh 1982). Intraspecific studies of the function of both duetting and solo songs are rare; however, such studies are important for understanding the functions of duets and solo songs for both sexes. In this paper we present a study of the function of song in Red-shouldered Blackbirds (*Agelaius assimilis*) a species that is endemic to Cuba and was formerly considered a race of the Red-winged Blackbird (*A. phoeniceus*; Garrido and Kirkconnell 1996). In Red-shouldered Blackbirds, male and female songs are similar and occur as both duets and solo songs (Whittingham et al. 1992). This is particularly fascinating because it is unlike most other duetting species which have sex-specific songs, and it provides an interesting contrast to the well studied Red-winged Blackbird. The song of both male and female Red-shouldered Blackbirds is similar to the song of the male Red-winged Blackbird (Whittingham et al. 1992). However, Red-shouldered Blackbirds differ from Red-winged Blackbirds in morphology and social behavior. Red-shouldered Blackbirds are socially monogamous and both sexes feed young with equal frequency, unlike Red-winged Blackbirds. In addition, Red-shouldered Blackbirds are less sexually dimorphic in size and plumage than Red-winged Blackbirds (Whittingham et al. 1992, 1996).

[1] Dept. of Biology, Queen's Univ., Kingston, Ontario, K7L 3N6 Canada.
[2] Author for correspondence. Present address: Dept. of Biological Sciences, P.O. Box 413, Lapham Hall, Univ. Wisconsin Milwaukee, Milwaukee, Wisconsin 53201.
[3] Museo Nacional de Historia Natural, Capitolio Nacional, La Habana, Cuba.

Several hypotheses for the function of avian song have been proposed and most apply to species that duet as well as to those in which individuals of either or both sexes sing solo songs. These include synchronization of reproductive activities, maintenance of contact between mates and mate location, territorial defense, mate guarding, mate attraction, and pair bond formation. Although these hypotheses are not mutually exclusive we can make specific predictions. (1) If song is important for the synchronization of reproductive activities, then songs by both sexes should be most frequent during the female's pre-fertile and fertile periods (Beletsky 1982, Ritchison 1986). (2) Song may be used to maintain contact between mates or to force a mate to be attentive (Wickler 1980, Hoelzel 1986, Kellner and Ritchison 1988, Smith 1994). This hypothesis predicts that songs should be most frequent in the presence of the mate and throughout the duration of the pair bond (i.e., potentially all year long in species with year-round or life long pair bonds). (3) Song may function in mate location, in which case we would expect songs to be most frequent when visual contact between pair members is occluded, perhaps in dense vegetation (Hooker and Hooker 1969, Thorpe 1972). (4) If territorial defense is a primary function of song then songs should be most frequent in response to territorial intrusions by conspecifics (Beletsky 1982, Kellner and Ritchison 1988, Arcese et al. 1988) and during territory establishment or during high risk of territory takeover (Baptista et al. 1993). If males and females cooperate in territory defense, then the similarity in the song and plumage of Red-shouldered Blackbirds may facilitate territory defense (e.g., Baptista 1978). (5) Song may function in mate guarding in which males or females attempt to deter their mate from attracting an additional partner (Sonnenschein and Reyer 1983, Montgomerie and Thornhill 1989, Møller 1991). In this case, we would expect song to be most frequent in response to intrasexual intruders during the fertile period. (6) A mate attraction and pair bond formation function suggests that song should be most frequent during courtship and pair formation and by unmated individuals early in the breeding season or in response to mate loss (Baptista et al. 1993, Hanski and Laurila 1993). In Red-shouldered Blackbirds, this function may apply to both sexes.

To investigate the function of duets and solo songs in Red-shouldered Blackbirds, we examined the social contexts in which songs were used and the behaviors associated with particular songs. Our results suggest that songs are important in pair bond formation and maintaining contact between mates.

METHODS

We studied Red-shouldered Blackbirds in the Zapata Swamp, Cuba, 162 km southeast of Havana. We observed the singing behavior of birds prior to the nesting period (5–17 April)

in 1992 and during the nesting period (25 May–4 June, 17–18 June, and 1–2 July) in 1993. During the pre-nesting period, birds were found only at Guama, a village of 12 small islands covered mostly by lawn, each with 6–8 cabins. Most islands have trees introduced from Australia, including bottlebrush (*Callistemon speciosus*) and *Eucalyptus* (spp.). During the pre-nesting period, Red-shouldered Blackbirds foraged throughout the islands, particularly in bottlebrush trees, but did not defend territories (see below). Guama is approximately 1 km via canal from the edge of Treasure Lake (16 km^2). During the nesting period we found birds only on their breeding territories which were established in the vegetation along the periphery of Treasure Lake. The vegetation consisted primarily of *Typha* spp., *Phragmites* spp. and *Sagittaria lancifolia*.

We caught 50 adult birds in mist nets, and all birds were banded with a unique combination of colored leg bands. We observed the singing behavior of second year (SY) and after second year (ASY; Pyle et al. 1987) adult males and females. The plumage of ASY males was entirely jet black except for the red-orange epaulet with a light yellow band along the distal edge of the epaulet. SY males were also black; however, the epaulet was orange interspersed with black feathers and lacked the distal yellow band. ASY females were also entirely jet black but lacked the epaulet. SY females had olivaceous feathers at the base of the lower mandible and whitish edges on the greater and middle wing coverts as well as on the under tail coverts (Whittingham et al. 1996).

Each morning between 07:30 and 11:00 h, we walked a circuit of four islands (in random order) on which foraging birds were found most commonly. A male and female were described as a pair if they were observed more than four times together and never observed separately. We observed each of 15 pairs during two to four independent observation periods. For data analysis, we used only observation periods which were ≥5 min in duration.

Singing behavior was observed until the pair flew away or until the group composition changed. In Red-shouldered Blackbirds, either sex sings solo songs or leads duets (a pair of songs, one song produced by each sex, overlapping or less than 1 s apart, and given repeatedly in sequence; Whittingham et al. 1992). During observations of singing behavior prior to nesting (April), we recorded (1) group size, (2) number of solo songs by males and females, and (3) number of duets led by male or led by female. We recorded the context of singing behavior as: (1) pair alone, (2) pair with additional female present, (3) pair with additional male present, or (4) pair with additional pair present. Additional birds were considered "present" when they were <2 m away from the focal pair. For each pair, the mean song rate from all observations was used so that each pair was represented only once in the data analysis.

We also observed singing behavior during the nest-building and incubation periods (May to July), and we recorded (1) number of solo songs or duets, (2) activity of male (perched, foraging), and (3) activity of female (collecting nesting material, building at nest, foraging). Observation periods during the nest-building and incubation periods were 30–240 min each, between 07:30–11:00 and 14:00–18:00 h.

During the pre-nesting and nesting periods, we recorded observations of aggressive behavior between individuals. Aggressive behaviors included bill tilting, flaring epaulets, and displacement of one individual by another (Nero 1956).

All birds observed as pairs were banded, and different pairs were observed in each year. Some unbanded individuals were included as "additional" birds present near pairs (see Table 2). Means were used when there was more than one observation period for each pair for each category. Means are presented with their standard errors.

RESULTS

During the pre-nesting season, birds were observed foraging around Guama either on the cabin lawns or in the bottlebrush trees. Of the 50

TABLE 1
NUMBER OF DUET AND SOLO SONGS/MIN (MEAN ± SE) OF RED-SHOULDERED BLACKBIRDS IN RELATION TO SEASON

Season[a]	N	Duets		Solo songs	
		Male leads	Female leads	Male	Female
Pre-nesting	15	0.23 ± 0.06	0.38 ± 0.06	0.93 ± 0.2	1.12 ± 0.2
Nest building	6	0.05 ± 0.01	0.01 ± 0.01	0.22 ± 0.04	0.14 ± 0.02

[a] Observations during the pre-nesting period were conducted in 1992 and observations during the nest building and incubation periods were conducted in 1993. N = number of pairs observed.

banded birds, 23 were ASY males, 10 were SY males, 9 were ASY females, and 8 were SY females. Birds were foraging either in pairs or in small groups (6.3 ± 0.6 birds). Of 22 foraging groups, 18 had an equal number of males and females. The remaining four groups had one or two additional birds present.

Aggression.—Red-shouldered Blackbirds singing at Guama during the pre-nesting period were not defending territories. Neither males nor females responded to duet or solo song playbacks conducted in the presence of both male and female taxidermic mounts (Whittingham, Kirkconnell and Ratcliffe, unpubl. data). In general, aggressive interactions were rare. We observed only five cases of aggressive behavior during the pre-nesting period at Guama: (1) bill tilting display (Nero 1956) between an SY male and an ASY male, (2) an ASY male supplanted two males singing near his mate, (3) a paired SY female supplanted and then chased another female, (4) an ASY intruder displayed his epaulets to a paired ASY male, and (5) a bill tilting display between two females. There was little evidence of overt aggression or territorial intrusions during the nesting period. Territorial boundaries on Treasure Lake were determined by monitoring the locations of males and females while they were foraging or singing. Throughout the nesting period, we observed only one male and one female on each territory (700 ± 128 m^2, N = 6). Unlike the territorial aggression commonly observed in Red-winged Blackbirds (Searcy and Yasukawa 1995), we observed only one instance where two males sang simultaneously at their common territorial border.

General vocal patterns.—Solo songs were more common than duets (Table 1). Both males and females sang solo songs more frequently than duets during the pre-nesting period (Student's *t*-test, males: $t = 9.89$, $P < 0.001$, females: $t = 7.68$, $P < 0.001$) and the nest building period (males: $t = 3.75$, $P = 0.001$, females: $t = 5.22$, $P < 0.001$). Duets and solo songs were more frequent during the pre-nesting period than during

TABLE 2

VOCAL BEHAVIOR OF RED-SHOULDERED BLACKBIRDS DURING THE PRE-NESTING SEASON[a]

Category	N	Duets		Solo songs	
		Male leads	Female leads	Male	Female
Pair type					
ASY male, ASY female	7	0.15 ± 0.1	0.23 ± 0.1	0	0.87 ± 0.5
ASY male, SY female	5	0.36 ± 0.1	0.67 ± 0.4	1.88 ± 0.1	1.05 ± 0.2
SY male, SY female	3	0.20 ± 0.1	0.47 ± 0.1	1.58 ± 0.3	0.85 ± 0.2
Social context					
pair alone	12	0.03 ± 0.03	0.33 ± 0.1	1.12 ± 0.3	0.18 ± 0.1
additional female	5	0	0.28 ± 0.2	0	3.13 ± 0.5
additional male	15	0.54 ± 0.2	0.58 ± 0.1	1.98 ± 0.3	1.23 ± 0.3
additional pair(s)	13	0.12 ± 0.05	0.24 ± 0.1	0.92 ± 0.3	1.07 ± 0.3

[a] Number of duets and solo songs/min (mean ± SE) were analyzed in relation to the type of pair members and the social context. Category refers to the factors used in one-way ANOVA tests (see text for results). N = the number of pairs observed.

the nest building period for both males and females (males: leading duets $t = 2.2$, $P < 0.05$, solo songs $t = 3.3$, $P = < 0.01$; females: leading duets $t = 5.3$, $P < 0.001$, solo songs $t = 4.2$, $P < 0.001$; Table 1).

Songs during pre-nesting.—During the pre-nesting period, singing behavior was analyzed according to the social context in which the song was given and pair type (N = 15 pairs; Table 2). The pair bond formation hypothesis predicts song will be more frequent during courtship or when pairs are newly formed. By definition, SY birds are in their first year after hatching (Pyle et al. 1987), and thus, SY individuals were most likely to be members of newly formed pairs participating in their first breeding season. We analyzed song in relation to pair type to see if pairs in which one or both members were SY individuals sang more frequently. Pair type refers to paired birds that were either (1) both SY individuals (N = 3 pairs), (2) an SY female and ASY male (N = 5 pairs), or (3) both ASY individuals (N = 7 pairs). Males led duets (one-way ANOVA, $F = 5.60$, df = 3, 41, $P < 0.01$; Table 2) and gave solo songs ($F = 4.49$, df = 3, 41, $P < 0.01$) more often when an additional male was nearby (<2 m away) than in other social contexts. Similarly, females gave solo songs most often when an additional female was nearby ($F = 11.12$, df = 3, 41, $P < 0.001$; Table 2); however, the rate of female duets was not affected by social context ($F = 2.37$, df = 3, 41, $P > 0.05$). Males paired to SY females sang more solo songs than males paired to ASY females ($F = 7.4$, df = 2, 12, $P < 0.01$; Table 2); however, pair type had little

TABLE 3

VOCAL BEHAVIOR OF RED-SHOULDERED BLACKBIRDS DURING THE NEST-BUILDING PERIOD[a]

Category	Duets		Solo songs	
	Male leads	Female leads	Male	Female
Female activity				
Collecting nesting material	0.04 ± 0.01	0.02 ± 0.01	0.39 ± 0.09	0.07 ± 0.02
Building at nest	0.05 ± 0.01	0.02 ± 0.02	0.17 ± 0.03	0.09 ± 0.02
Foraging	0.09 ± 0.04	0.02 ± 0.02	0.17 ± 0.03	0.09 ± 0.02
Male activity				
Perched	0.07 ± 0.02	0.01 ± 0.01	0.35 ± 0.03	0.20 ± 0.08
Foraging	0.05 ± 0.01	0.01 ± 0.01	0.15 ± 0.06	0.19 ± 0.04

[a] Number of duets and solo songs/min (mean ± SE) were analyzed in relation to male and female activity (see methods).

influence on the rate of duets or female solo songs (all $F < 1.29$, df = 2, 12, all $P > 0.3$).

Songs during the nesting period.—In all pairs of birds (N = 6) observed during the nesting period both individuals were ASY. Thus, we did not include pair type as a factor in analyzing song rate during this period. During the nest-building period, female song was observed during three main activities: foraging, collecting nesting material, or building the nest. Males were either foraging low in the vegetation or perched overlooking the territory. The rate at which males and females led duets was not related to male or female activities (all $F < 3.6$, all $P > 0.07$; Table 3). However, during the nest-building period, males sang significantly more solo songs when they were perched than when they were foraging ($F = 9.01$, df = 1, 10, $P < 0.02$). Males also sang more solo songs when females were collecting nesting material than when females were at the nest or foraging ($F = 9.04$, df = 2, 15, $P < 0.01$; Table 3).

DISCUSSION

Songs in Red-shouldered Blackbirds were most common prior to the nesting period when birds were not on breeding territories. Intrasexual interactions appeared to influence the rate at which males led duets and the rate at which both sexes sang solo songs in the pre-nesting period. Furthermore, the high rate of solo songs given by males paired to SY females suggests that the recency of the pair bond influenced male solo song rate. During the nesting period, intrasexual interactions were rare and male songs were most common when males were perched on their territory and females were collecting nesting material. We suggest that

duets and solo songs are important in intrasexual interactions and may function in pair bond formation during the pre-nesting period. In addition, songs may be important in maintaining contact between mates during the nesting period.

Our observations do not support the synchronization of reproductive activities or mate location hypotheses for the primary function of song. Contrary to the prediction of the synchronization hypothesis, the rate of duet and solo songs, for both sexes, was lower during the female's fertile period (i.e., nest building). In other species, singing prior to the female's fertile period stimulates hormones which may advance nesting (Kroodsma 1976, Morton et al. 1985, Cheng 1992). We do not know if song functions as a sexual stimulant in this manner in Red-shouldered Blackbirds, but this idea warrants further investigation.

A mate location function is likely to be important in tropical species nesting in dense vegetation where mates are often out of sight of each other (Hooker and Hooker 1969). It is unlikely that this is a primary function of song in Red-shouldered Blackbirds, because when songs were most frequent pairs foraged together in open lawn areas prior to the nesting season.

In many species, duets as well as male and female solo songs play an important role in intrasexual aggressive interactions associated with territorial defense (e.g., Payne and Skinner 1970, Baptista 1978, Farabaugh 1982, Sonnenschein and Reyer 1983, Beletsky 1983). Similarly, in Red-winged Blackbirds, male songs function primarily in intrasexual interactions associated with territorial defense and mate attraction (e.g., Searcy and Yasukawa 1990), and female songs appear to be important in intrasexual aggressive interactions (Beletsky 1983). Both sexes of Red-shouldered Blackbirds sang frequently during intrasexual interactions prior to the nesting period while foraging away from their breeding territories, suggesting that territorial defense was not a primary function of song at this time of year. Although territorial aggression may be rare and song rate was low during the nesting period, most male songs occurred when they were perched, suggesting that solo songs could be associated with advertising territory occupancy. Red-shouldered Blackbirds at Guama do not seem to defend territories year round, and as a result, it is possible that songs are more important in territorial defense when borders are first established or when borders change (e.g., when a neighboring male disappears). To investigate this possibility, it will be necessary to make observations of territory establishment and conduct experiments that temporarily remove males from territories during the nesting period.

Both duets and solo songs seem to be important in intrasexual interactions, suggesting that these songs may function in mate guarding.

Males may sing in response to the presence of additional males to deter extra-pair copulations and protect their paternity (e.g., Farabaugh 1982, Montgomerie and Thornhill 1989, Møller 1991). This is unlikely to be a primary function of male song in Red-shouldered Blackbirds because song rate was greater during the pre-nesting period and lower during the female's fertile period (i.e., nest building). In contrast, females may sing in response to the presence of conspecific females to deter their mates from pairing with additional females (i.e., polygyny; Sonnenschein and Reyer 1983). The risk of polygyny will not necessarily be limited to the female's fertile period because pair bonds are apparently formed well before the nesting period. Polygyny and the consequent loss of male parental care could be costly to females because male Red-shouldered Blackbirds contribute a substantial amount of parental care to nestlings (Whittingham et al. 1996). Polygynous male Red-winged Blackbirds often assist only one of several mates, and the lack of male parental care reduces fledging success (e.g., Whittingham and Robertson 1994). It is possible that females are singing more frequently prior to nesting to advertise their mate's mated status; however, it is unlikely that males are singing frequently at this time to protect their paternity and deter extra-pair copulations.

A role for song in mate attraction and pair bond formation is suggested in many species because unpaired individuals sing frequently, reducing the rate of songs after pairing (Quaintance 1938, Marshall 1964, Catchpole 1973). In addition, individuals of either sex that lose their mate (i.e., widowed) may increase their song rate while trying to attract another mate (Baptista et al. 1993, Hanski and Laurila 1993). Since SY individuals are more likely to be members of newly formed pairs, the high rate of solo songs by males paired to SY females suggests that these songs may play a role in pair bond formation in Red-shouldered Blackbirds. At present, we lack information on the vocal and social behavior of unpaired Red-shouldered Blackbirds, but natural and experimental (i.e., via temporary removals) observations of the mate attraction process will help clarify the important functions of song in this species.

In many species of birds, individuals do not stop singing once they become paired, although song rate may change. A combination of the pair bond formation and maintenance hypotheses predicts songs will be more frequent during pair formation and less frequent during the maintenance period (Arrowood 1988). In Red-shouldered Blackbirds, singing by both sexes continued throughout the nesting season at a significantly lower rate than during the pre-nesting season, consistent with a function in pair bond formation and maintenance. Furthermore, both sexes in this species sing during the winter (A. Kirkconnell, pers. obs.). Pair bond maintenance or

maintenance of contact between mates is often suggested as the primary function for year round singing in many duetting species (Hooker and Hooker 1969, Payne and Skinner 1970, Wickler 1980, Farabaugh 1982, Sonnenschein and Reyer 1983).

A comparison between Red-winged and Red-shouldered blackbirds reveals some differences and similarities in the function and context of their songs. Similar to Red-shouldered Blackbirds, the song of male Red-winged Blackbirds functions primarily in mate attraction and pair bond formation (Searcy 1988, Searcy and Yasukawa 1995); however, in Red-winged Blackbirds this occurs primarily on their breeding territories, whereas, in Red-shouldered Blackbirds this occurs prior to territory settlement. Experiments in Red-winged Blackbirds illustrate that male song has an important function in territory defense (reviewed by Searcy and Yasukawa 1995). In contrast, song in Red-shouldered Blackbirds, by either sex, was infrequent following territory settlement, suggesting that territorial defense may not by a primary function of their songs. The song of female Red-winged Blackbirds is unlike the song of female Red-shouldered Blackbirds (Whittingham et al. 1992); however, in both species song seems to be important in intrasexual interactions. For female Red-winged Blackbirds this occurs primarily on the breeding territories (Beletsky 1983), while for female Red-shouldered Blackbirds it is associated with interactions prior to the nesting period.

The similarities between male and female Red-shouldered Blackbird duet and solo songs suggests similarities in function (Baptista 1978). Our data suggest that duet and solo songs of both sexes are important in intersexual and intrasexual interactions prior to the nesting period. Additional information on the vocal and social behavior of Red-shouldered Blackbirds throughout the year will be necessary to understand fully the function of duet and solo songs. Our observations suggest that the processes of mate attraction and territory establishment will be an important focus.

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SOME ASPECTS OF THE BREEDING BIOLOGY OF THE BLACK SWIFT

MANUEL MARÍN

ABSTRACT.—Nests of the Black Swift (*Cypseloides niger*) usually are associated with water. Clutch size is invariably one. Incubation is by both adults and lasts ca 24 days, and the nestling period lasts ca 48 days. Nestlings reach and surpass adult mass before fledging and adult size in linear measurements after fledging. The species is single-brooded, probably because of the long incubation and nestling periods that must be accomplished in a brief period of time. *Received 13 Aug. 1996, accepted 11 Dec. 1996.*

RESUMEN.—El Vencejo Negro construye sus nidos en lugares húmedos cerca de agua. Invariablemente la postura es de un huevo, que es incubado por ambos sexos por un período de ca 24 días. El período de crecimiento dura ca 48 días. Las medidas de crecimiento se refieren por un lado a las que adquieren el tamaño de adulto antes de salir del nido y por otro lado las medidas lineares que adquieren el tamaño de adulto fuera del nido. El hecho de que esta especie tenga una sola nidada es debido a la larga incubación y al largo período de crecimiento, que debe ser completado en un tiempo restringido. Durante el crecimiento el polluelo acumula grasa por tres posibles razones: seguridad contra lo impredicible de la disponibilidad de alimento, ayuda para la termoregulación en el frío ambiente de los nidos y energía para su vuelo migratorio que posiblemente comience al salir del nido.

As the most aerial of birds, swifts are difficult to observe and identify in the field. Because access to nesting sites is often difficult, large gaps exist in our knowledge about the biology of many swifts. The Black Swift (*Cypseloides niger*) is found locally in northwestern North America south throughout Middle America and the West Indies (AOU 1983). Some observations of its nesting biology have been published (Vrooman 1901, 1905; Michael 1927; Dixon 1935; Knorr 1950, 1961, 1962; Knorr and Knorr 1989), but the most complete works on its breeding biology emphasize only its breeding distribution (Foerster 1987, Foerster and Collins 1990), leaving many aspects unknown. The goal of this study was to elucidate previously unstudied or little-known aspects of the breeding biology of the Black Swift.

STUDY AREA AND METHODS

From 1990 to 1992, I studied Black Swifts in the San Jacinto Mountains, Riverside Co., southern California. The habitat surrounding the study site was montane forest. Predominant tree species were ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and Coulter pine (*Pinus coulteri*). Other species present included incense cedar (*Calocedrus decurrens*) and white alder (*Alnus rhombifolia*). In the lower parts

[1] Museum of Natural Science and Dept. of Zoology and Physiology, Louisiana State Univ., Baton Rouge, Louisiana 70803 and Western Foundation of Vertebrate Zoology, Camarillo, California 93012.

TABLE 1
DIMENSIONS AND MASS OF BLACK SWIFT EGGS (N = 50)

Feature	Mean	SD	SE	Range
Length (mm)	28.7	1.06	0.15	26.3–31.8
Width (mm)	18.8	0.52	0.07	17.4-19.7
Mass[a] (g)	5.5	—	—	5.1–6.4[b]

[a] Calculated from mean egg measurements; see methods.
[b] Mass from the smallest and largest egg from the sample.

of the canyon below the study site, montane chaparral was present, with predominant species on south-facing slopes being scrub interior live oak (*Quercus wislizenii*), black oak (*Q. kelloggii*), live oak (*Q. chrysolepis*), manzanita (*Arctostaphylos* spp.), and chamise (*Adenostoma fasciculatum*). More detailed information on the vegetation of the area can be found in Barbour and Major (1977).

The study site was a natural cave about 15 m deep and ca 7–8 m in height formed by the merging of large boulders in the North Fork of the San Jacinto River at 1500 m (ca 33°45′N, 116°43′W) near the town of Idyllwild. The stream flows year-round, forming a waterfall over the boulders, but flow varied substantially among years and seasons. The inside of the cavern had a substantial flow of water through a side wall, forming a small waterfall and several minor drips from the roof. This internal flow of water also varied among years.

Field data were collected during three visits in 1990, once each in June, August and September. In 1991 data were collected from late May to mid-September, in 21 visits. During incubation and nestling periods, nests were inspected at 1–6 day intervals. During 1992, the site was visited once in May and 15 times from early July to late September, usually every 1–3 days. The third year was used to supplement data from previous years and to carry out a preliminary twinning experiment. This experiment was conducted at two different stages (see below). Because I had to leave the area before the end of the experiment, J. Schmitt and W. Wehtje measured mass, wing, outermost primary, and tail from age 38 until fledging.

I weighed body mass (to 0.1 g with a Pesola spring balance), and measured wing length (flattened), extended wing, 10th primary length, and tail length to 0.5 mm using a stopped wing ruler. Other measurements, such as tarsus length, exposed culmen, head width, foot span, and gape width, were measured to the nearest 0.1 mm with dial calipers (following Baldwin et al. 1931, Marín and Stiles 1992). Nestlings were measured mostly in the morning between 09:00 and 11:00 h. Any measurement taken later than 12:00 h. was given a half-day increment. Colors are those from Smithe (1975, 1981), with number and name (e.g., 83 Dark Neutral Gray). Egg shapes follow Preston (in Palmer 1962). Eggs measurements (Table 1) are mainly from museum specimens, measured to the nearest 0.01 mm with digital calipers. Average egg mass was calculated from museum specimens, using the formula ($M = K \cdot L \cdot B^2$), were L = length, B = breadth, and k was calculated by regression using fresh egg mass (Hoyt 1979). Temperature within the cave was measured with a portable thermometer placed upon arrival near the center of the cave and read just before leaving.

Adults had been banded by K. Foerster and C. Collins (see Foerster 1987), allowing recognition of individuals. On eight evenings, mist nets were set at dusk at the cave entrance in order to capture adults and to obtain an indication of the population size, body masses, and morphological measurements. Measurements of adults from the study site were taken

TABLE 2
MORPHOLOGICAL MEASUREMENTS OF BLACK SWIFTS[a]

Feature	Mean	SD	N
Mass (g)	44.1	± 2.49	(16)
Tarsus length (mm)	14.5	± 0.56	(9)
Foot span (mm)	21.6	± 1.14	(9)
Gape (mm)	16	± 0.92	(14)
Exposed culmen (mm)	6.6	± 0.44	(14)
Head width (mm)	21.6	± 0.41	(14)
Wing (mm)	168.8	± 3.16	(16)
Extended wing (mm)	187.5	± 7.47	(15)
Outermost primary (mm)	127.3	± 2.56	(11)
Tail length (mm)	55.4	± 3.18	(15)

[a] Table follows the same sequence as in Fig. 1 A–J.

as described above (Table 2). To complement the field data, other data were gathered from museum specimens and egg data cards (see acknowledgments).

RESULTS AND DISCUSSION

Nests.—As with other cypseloidine species (Snow 1962; Collins 1968; Whitacre 1989; Marín and Stiles 1992, 1993), Black Swifts breed in close proximity to water. The nests studied near Idyllwild were in the dim interior of a single large cave and placed in small niches formed by ledges or knobs. Nests of the Black Swift are almost invariably located in dim, moist areas away from sunlight (Knorr 1950, 1961, 1962; Legg 1956; Foerster 1987), although four of five active nests found by Hunter and Baldwin (1962) in Montana received direct sunlight late in the afternoon.

The angle or position of the nest depended on the angle of the substrate, which varied from a flat surface to a 45° angle. Height above ground varied from 0.4 to 6 m. The nest shape varied from a half-cup or inverted cone to a cup-shape depending on the substrate. The former was observed when the nest was attached to a knob, the latter shape when it was placed on a ledge. External measurements were highly variable, depending on substrate and manner of attachment, but the internal diameter was relatively uniform, averaging 9.0 cm (N = 12). Hunter and Baldwin (1962) reported 9.1 cm for Montana and Holroyd and Holroyd (1987) 8.5 × 7 cm for British Columbia, Canada. The nests near Idyllwild (N = 12) were composed entirely of mosses, with some mud in the base and a few pine needles in the lining. One species of moss (*Scleropodium touretii*) was identified on the nests, although others may occur. However, Foerster (1987) found the same species of moss in five of six nests. This species

of moss was found growing commonly in compact to spreading mats in soil on the cave walls.

Although mosses are the main nesting material in most Black Swift nests, it is not the only material reported. In California, coastal nests differ greatly from inland nests. Indeed, the first two nests described by Vrooman (1901, 1905) differed from many; he found in both cases that the egg was laid in a slight depression in the mud on sea-cliffs. Furthermore, Vrooman (1905) stated that "there was no nesting material whatever." Another coastal nest found in a sea cave was constructed of 90% green seaweed (Legg 1956). Egg data cards for the coastal nests show great variation in nest material and construction. Those from the California coast in Santa Cruz County (N = 51) indicated that 26% of the nests were built from seaweed, 4% were a mix of mosses and seaweed, 35% were composed of mosses, and 35% had no nest material at all. The inland nests (N = 43) all involved nesting material, especially mosses, although fern tips were mentioned for some. Pine needles as lining material were commonly mentioned in the egg-data cards for the inland nests; these were found in all nests in the San Jacinto Mountains.

I observed nest construction in detail only once, on 8 June 1991. One bird was observed gathering moss from the cave wall. This individual had lost its nest during the previous winter. The bird clung to the wall, wings extended, and gathered moss with its bill, similar to the manner of other cypseloidines (cf Marín and Stiles 1992). The bird did not use much nesting material, and the nest was built on a flat surface. I am not certain how many days it took to build its nest, but when first observed, construction had already begun, and by June 16 the nest had a fresh egg. During this study, each pair reused its old nest every year, adding small amounts of new material. There is only one other account of nest construction, on an egg data card (MVZ # 4309); according to the collector, C. P. Streator, "the nest was built in four days."

Based on Foerster's (1987) work, the San Jacinto Mountain nests had been used for ten years or more. During the three years that I worked there, the exact same sites were used every year and by the same birds; however, some birds rotated position or changed mates. A nest that Foerster studied in 1985–1986 was present in 1990. During 1991, early in the season there was a heavy rain and water destroyed the nest. The same bird constructed a new nest higher in the cave on a ledge that possibly was an older, unoccupied site. The only mate change recorded in the cave occurred in 1992, when a first-time breeder, present the previous year as a possible floater, mated with an older bird that already had a nesting site from previous years.

Eggs and incubation. After nests were completed, roughly 10–14 days

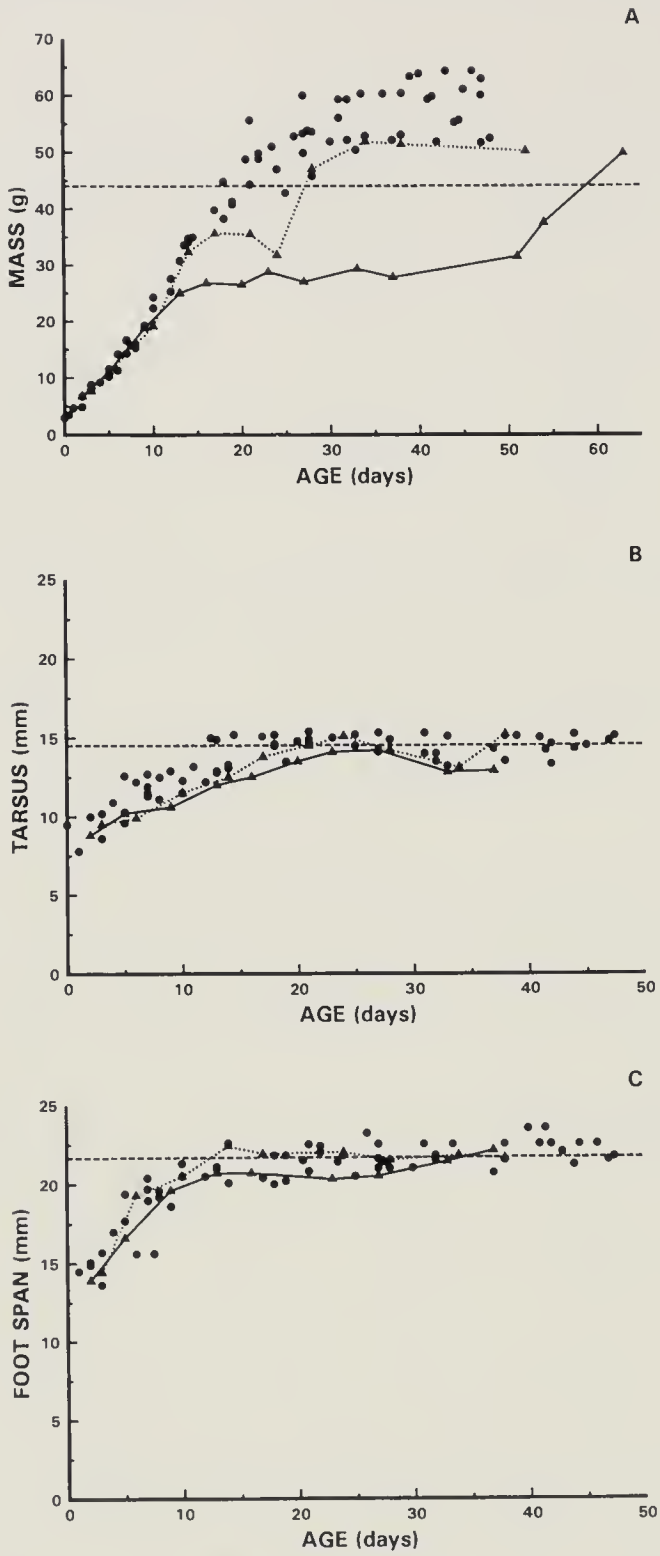

FIG. 1. Growth curves of ten parameters in the Black Swift. Dashed horizontal lines represent average adult size and correspond to numbers from Table 2. Dotted and solid lines in the growth curve represent the twins experiment (see text).

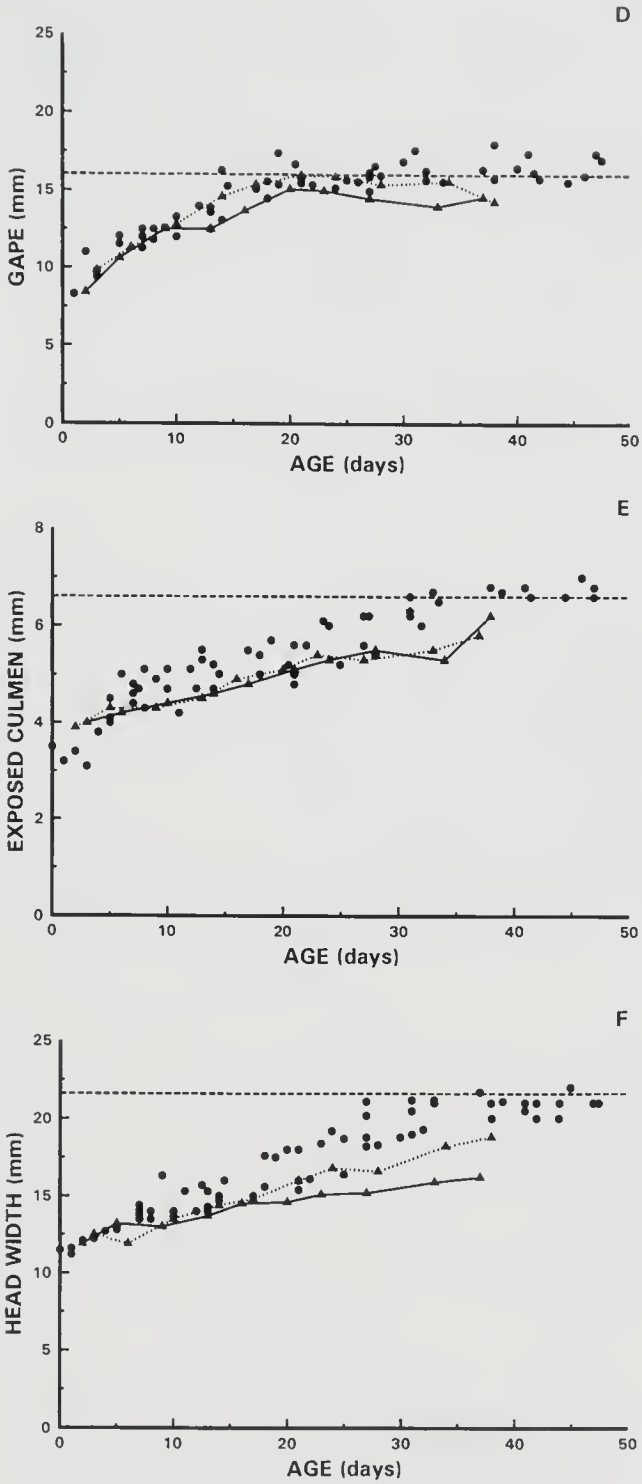

FIG. 1. Continued.

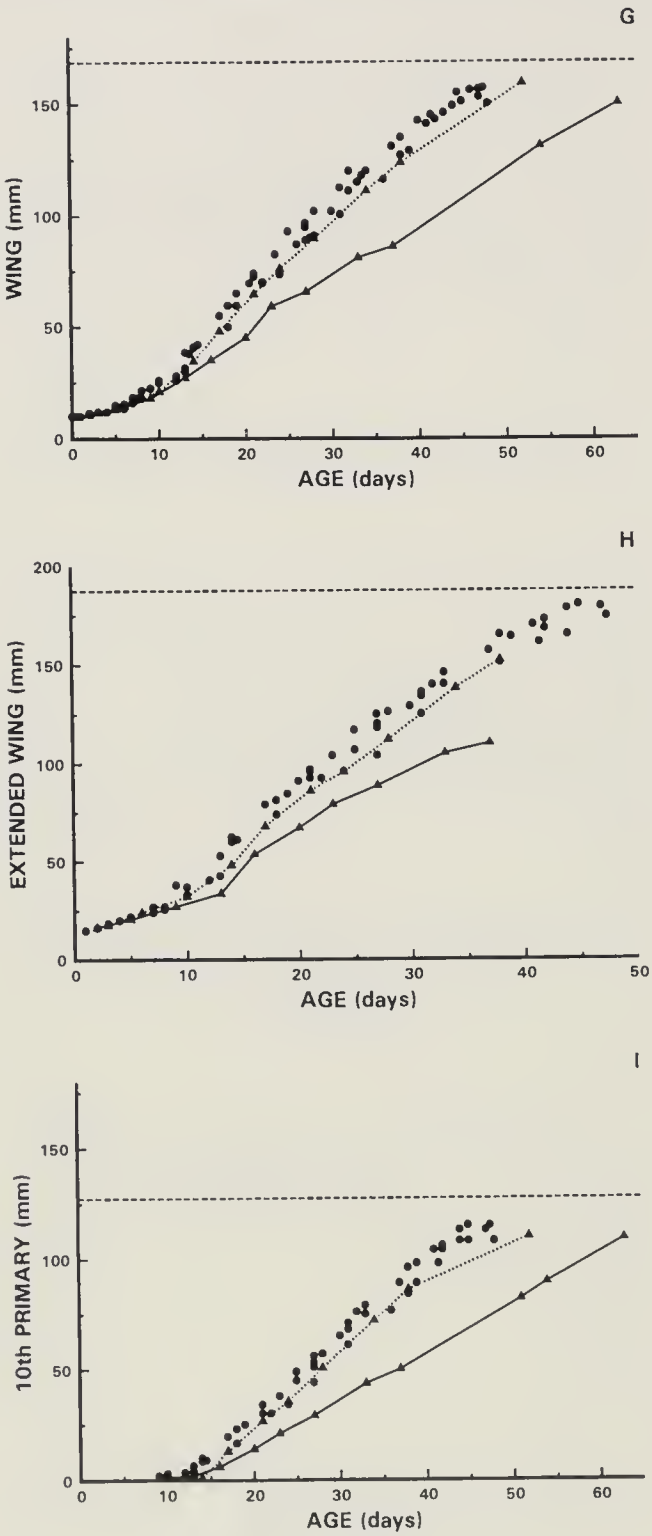

FIG. 1. Continued.

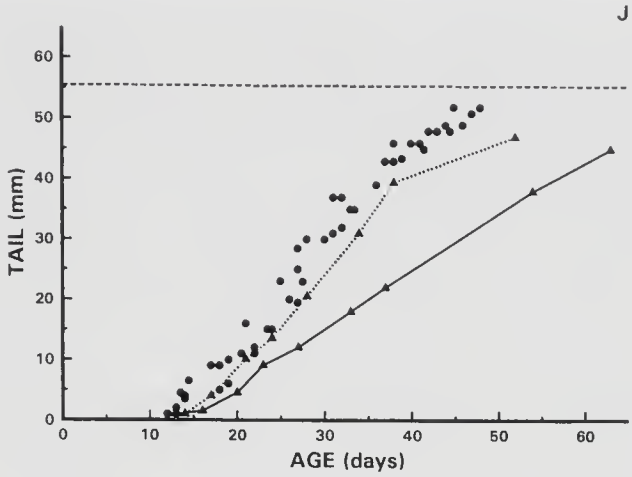

FIG. 1. Continued.

elapsed before eggs were laid. During this period, I observed on six occasions one of the birds, presumably the female, spent more time on the nest, although it is uncertain how many hours were involved. This pair member behaved in each case as if it were incubating, but no egg was found.

All clutches observed at this site were of single eggs (N = 16), as elsewhere in the species (e.g., Bent 1940, Foerster 1987). The eggs (N = 50) were dull white, and their shapes were subelliptical (56%), long subelliptical (20%), oval (16%), or long oval (8%). For egg measurements and mass see Table 1.

During the three years of study, all eggs (N = 16) were laid in June, most by mid-June. Twice, once in 1990 and once in 1991, eggs were lost, and although both eggs were fresh, they were not replaced. I was unable to fully document incubation pattern, but incubation spells were long, often more than 4 h. Incubation periods at six nests averaged 24 days (range = 23–26 d). The only two previous reports on the incubation period of the Black Swift (Murphy 1951, Legg 1956) estimated the incubation period at 24 and 27 days, from one nest each, in Colorado and California, respectively.

The eggs were never left uncovered, and the birds sat closely when nests were approached. Mates shared incubation and brooding. Data from four nests indicated that one member of a pair, presumably the female, spent somewhat more time incubating: in the first nest, one of the mates was hand caught six of nine times or 66% of the time, in the second nest three of five times or 66.6% of the time, on third nest one of the birds was captured seven of 11 times or 63.3% of the time, and in the fourth nest four of eight or 50% of the time.

I studied the full development of nine nestlings, not including those

used in twinning experiments (see below). Two nestlings were followed from hatching day zero, two from day one, and three from within 2–5 days of hatching through fledging (Fig. 1A–J). The nestlings at hatching were naked and helpless, with eyes closed, and they weighed 3.1–3.5 g. The hatched eggshells were not removed by the parents, but either rolled out or stayed near the nest until degradation. At hatching, the nestlings' skin was flesh colored ventrally and tinged gray dorsally with subcutaneous black dots. The feet were soft flesh-pink in color, with gray, white-tipped claws, and were well developed (64.6% of adult size). The bill was blackish with a conspicuous white egg-tooth. Disappearance of the egg-tooth varied from age 18 to 33 days (mean = 24 days, N = 6). Body mass increased almost linearly from hatching until reaching about 113% of adult size (Fig. 1A). Adult mass was attained at age 18 to 22 days (mean = 20, N = 7). Maximum body mass was reached, on average, by day 39 (range = 33–45 days, N = 7). No swifts fledged at less than 50 g or 113% of adult size. The maximum mass reached by any nestling was 64.3 g or 148% of adult mass. Tarsus, foot span, and gape all reached adult size at an early age (Fig. 1B–D).

The eyes were barely open by day 7–8 and fully open by day 14–16. Semiplumes were sprouting over the head, back, and upper chest by 6–7 days. By 13–14 days, the nestlings were nearly fully covered with dark-gray, downlike semiplumes, but these were still growing on the sides of the forehead which were noticeably naked. These downlike semiplumes (near 83 Dark Neutral Gray) were darker than those of *Streptoprocne* spp. but lighter than those of other *Cypseloides* spp. (cf Marín and Stiles 1992). The forehead feathers began to emerge between 18–21 days. The secondaries emerged by 8–10 days, broke their sheaths by day 13, and were fully grown by 32–33 days. The outer primaries began to emerge by day 13 and grew steadily until fledging (Fig. 1G). Nestlings usually fledged by day 48, or when the 8th primary was fully grown and the 10th was 90% of adult size (Fig. 1I). The rectrices began to sprout by age 12–14 days, and sheaths were broken by 20–22 days. The rectrices reached about 90% of adult size by fledging time (Fig. 1J). The fledgling plumage was uniformly blackish (between 82 Blackish Neutral Gray and 119 Sepia), with most feathers having a white edging that produced a scalloped effect. The only feathers or areas without white edging were the two outermost primaries, the outermost underwing primary coverts, and those of the nape, hindneck, throat, upper breast, and the side of the neck. Most white edging wore away rapidly, but in some areas, primarily the abdomen, vent and crissum, the white tipping was broader, and based on museum specimens, I suspect that this would persist for at least three years and possibly more.

Twinning experiment—To determine the capacity of the parent to feed a supranormal brood size and to test the growth constraints imposed on the chick, I conducted twinning experiments. In cypseloidine swifts, and probably in most swifts, brooding seems to be a critical factor in the first 13–14 days of life, or until acquisition of thermoregulatory ability. Foerster (1987) noted that the body temperature of a 4-day-old Black Swift dropped 15°C in 28 minutes. Collins (1968) found that the body temperature of the Chestnut-collared Swift (*Streptoprocne rutila*), also a cypseloidine, approached an asymptote, hence thermoregulatory ability, by age 12–13 days, coinciding with the full growth of the downlike semiplumes. In several species of swifts, mortality is higher in the first 10–13 days of life (Lack and Lack 1951, Tarburton 1986, Francis 1987, Malacarne and Cucco 1991). Following these parameters as a guideline, I conducted experiments in two parts: (1) at the point when I assumed that young had acquired thermoregulatory ability (or close to it) at age 13–14 days, when the semiplumes were well grown, and (2) before 13–14 days, when they were assumed not to be homeothermic. The first set of twins (the added nestling A, dotted line, and the original nestling B, solid line, on Fig. 1A–J) were within a half day of being the same age. All parameters were measured from hatching until age 38, but only four parameters were measured until fledging. During the first 10 days of the experiment, fluctuations of the growth curve implied that nestlings competed for food (Fig. 1A). From the 10th day of the experiment (at 25 days of age) to the 38th day, the larger nestling (A) became aggressively dominant. From 25 days of age onward, nestling B began to shiver as soon as it was separated from its sibling, an indication that most energy or food was allocated for growth rather than temperature regulation. Nestling A increased its body mass almost linearly, reaching asymptotic mass at age 34. Nestling B remained at about 25–28 g, for about 39 days, until nestling A fledged at age 52 (Fig. 1A). Nestling A was only four days behind the normal nestling period, fledging at 50.1 g (or 113% of adult size). Nestling B increased its body mass linearly (1.65 g/day) from day 52 to 63, reaching the same fledging mass as nestling A in 11 days. The minimum fledging mass for this species seems to be ca 50 g.

Surprisingly, both nestlings grew within the normal measurements for some parameters, e.g., tarsus and foot span, (Fig. 1B, C). Gape, exposed culmen, and especially head width, grew somewhat more slowly (Fig. 1D–F). From day 11 onward, nestling B lapsed progressively behind in wing and tail measurements (Fig. 1G–J), reaching fledging mass and size dimentions 15 days later than the average nestling.

The second twinning experiment was undertaken when the nestlings were eight days old. The added nestling disappeared within three days,

probably removed by a human. The small number of nests precluded additional experimentation.

Fledging.—Four Black Swift nestlings fledged in the morning before 8:00 h. Morning departure, often before 8:00 h, is typical in the Common Swift (*Apus apus*) and also in many other swift species (reviewed by Lack 1973). The cue for fledging might be attainment of a particular mass. In the twinning experiment, the parents did not abandon the second nestling until it reached the same mass as its artificial sib.

In central and southern California, the Black Swift seems to migrate primarily in small groups, and migration lasts for about a month from late August to mid September (Rathbun 1925, Marín, unpubl. data). At San Jacinto, most birds ceased to frequent the cave during the last week of August or first week of September, with the latest observation in all three years being 9 September. Foerster (1987) found a similar chronology for southern California. Once youngs fledged, no adult or young birds were observed in the cave. Because suitable roost sites are limited, it seems likely that if the birds had remained anywhere in the vicinity after fledging, they would have continued to use the cave as a roost. Therefore, it seems more likely that all birds, including young, left for migration as soon as the young fledged. To date there is no evidence that Black Swifts roost aerially as does the Common Swift (*Apus apus*) at times. In the latter species the young do not return to the nest after they fledge, presumably migrating immediately (Lack and Lack 1952). A juvenal Common Swift banded in Britain that fledged on 31 July was found four days later 1275 km away in Spain (Cramp 1985).

The location of the wintering grounds of the Black Swift is still a mystery; however, the recent records by Stiles and Negret (1994) in Colombia suggests that they winter much farther south than previously thought.

Knorr (1961) proposed five ecological requirements for nest sites of the Black Swift: water, high relief, inaccessibility, unobstructed flyways, and darkness. Marín and Stiles (1992) reexamined these "requirements" and concluded that cypseloidine swifts breed in close proximity to water for two major reasons: (1) to have a more constant environment to ameliorate daily temperature changes around the nest and (2) to have high humidity for nest attachment to the substrate. Three of Knorr's (1961) five requirements (high relief, inaccessibility to the nest by terrestrial predators, and unobstructed flyways) were believed to be secondary consequences of nesting behind or next to waterfalls.

The nests examined in this study varied from 0.5 to 8 m or more in height above the cave floor. During 1990, a very dry year, we found remains of one adult from a low nest, probably eaten by a terrestrial

predator, as the remains were well inside the cavity. Some nests were far from "a clear flyway," and the birds maneuver well in enclosed spaces. Lastly, there appears to be no reason why darkness *per se* is not also simply a byproduct of site selection.

The internal temperature of the cave throughout the field season fluctuated no more than 2°C. Readings taken at night and very early in the morning differed only 1–2°C from those taken during the day. Furthermore, cave temperatures throughout the season were just above the minimum external temperature. External temperatures fluctuated daily on the order of 10–20°C. Similarly, Foerster (1987) reported steady temperatures for the same site. He also reported an increase in temperature between months, with a significant difference between the upper and lower nests in the cave: throughout the season upper nests had a maximum temperature of 9.5°C and lower nests, 5.5°C. Foerster (1987) reported a range of humidity from 54 to 96% throughout the season. I took only a few humidity readings, mainly during the early part of the 1992 season; these were in the 80–90% range but decreased as the summer advanced. Most nests were in the lower, wetter part of the cave, where temperature variation was less. This effect certainly would assist nestlings in maintaining a steady body temperature when adults are away from the nest.

Dawson (1915), while collecting nests of Black Swifts along the coast in Santa Cruz County, California, noted that the area had the same cold and moisture found at higher elevations. Most egg collectors remarked on the egg data cards how damp and muddy the nest sites were. All the inland nests were made of mosses, and the common characteristics were "wet" and "green"; these same words were applied to the coastal nests made of seaweed. On the data cards for the coastal nests with no nest materials, words such as "damp" and "muddy" were mentioned frequently. In fact, all sites so far reported present the same microclimatic conditions.

Several California egg collectors, including as L. T. Stevens, W. E. Griffee, and A. G. Vrooman, visited particular Black Swift nesting sites for many years and reported that these sites were regularly used by the species. For example, L. T. Stevens wrote on an egg data card that the same nest was used for 21 years, and W. E. Griffee reported one used for 13 years or more. Collins and Foerster (1995) reported a bird using the same site for at least 10 years. Although there is no evidence that the same bird used the same nest, the specific site of the nest seems to be a critical factor. Nest microclimate influences daily energy requirements which can be crucial to the adult during incubation and to the young when adults are away foraging (Gill 1995).

Although the humid nest site is important for diel temperature amelio-

ration for the Black Swift, it is evidently not as important for attachment of the nest to the substrate as is the case for the Spot-fronted Swift (*Cypseloides cherriei*) and the Chestnut-collared Swift (*Streptoprocne rutila*) (see Marín and Stiles 1992), because nest placement and construction varies greatly in Black Swifts. Most nests, particularly the coastal ones, were built on flat surfaces; 35% (N = 49) of these nests had no structure built by the swifts. This may serve to eliminate time and energy involved in nest construction, because nests built at an angle would need more specific construction material and probably would take more time in the accretion of the mosses (Marín and Stiles 1992). The lack of nest construction and nest site variability may also result from lack of competition with other species of cypseloidines for nest sites or from strong intraspecific competition for quality nest sites. Lack of nest construction has been found also for the White-naped Swift (*S. semicollaris*) and the White-collared Swift (*S. zonaris*) in Mexico (Whitacre 1989) and for the White-collared Swift in Costa Rica (Marín and Stiles 1992); but for these species lack of nest construction might reflect intraspecific rather than interspecific competition for quality sites. However, because all cypseloidines nest in similar sites, nest substrate, angle and body mass can be an important means of partitioning nest sites (Whitacre 1989, Marín and Stiles 1992).

The Black Swift lays a single egg, and, if this egg is lost, there is no attempt to replace it. Single-broodedness is rare among birds and occurs in some seabirds and some raptors (Wynne-Edwards 1955). The two one-egg cypseloidines, the sedentary tropical species, White-chinned and Spot-fronted swifts studied in Costa Rica by Marín and Stiles (1992), replaced lost eggs within a month or so. Black Swift egg mass was lighter relative to body mass (12.5%) than in these other one-egg *Cypseloides* spp. (16.4 and 16.7%, respectively, Marín and Stiles 1992). Thus the lack of egg replacement in the Black Swift may be related not to egg size but to the fact that the long incubation and nestling periods must be accomplished in a more restricted time period than in the tropical one-egg species.

As with other cypseloidines, Black Swift nestlings developed slowly, slower than the species of *Streptoprocne* but faster than other two *Cypseloides* species so far studied (see above). It is uncertain whether this is an effect of latitude or body size. The larger species in this group tend to grow faster, which is contrary to the Class Aves as a whole (Marín and Stiles 1992). In the Black Swift, different aspects of nestling growth fell into three basic patterns: non-linear measurements that acquired adult size within the first 10–15 days of life (Fig. 1A–D); non-linear measurements that reached adult size late in the breeding cycle (Fig. 1E, F); and linear measurements that reached adult size after fledging (Fig. 1G–J).

The first four measurements (Fig. 1A–D) were probably the most critical in acquiring adult size early in the nesting period. The initial fast growth of mass is probably linked to acquisition of homeothermy, whereas rapid growth of tarsus and foot span is associated with avoiding rolling out of the nest and that of gape size with intake of large food boluses.

Mass, wing, and tail length measured by Foerster (1987) presented a trend similar to that of the present work.

Manipulations to test the adaptative nature of clutch size and growth constraints have shown that many species of birds can raise an extra nestling (see below). However, experiments on species with small clutches have been conducted primarily on seabirds (reviewed by Ydenberg and Bertram 1989, Stearns 1992). The single experiment carried out on one-egg swifts showed that 29% of the manipulated nestlings survived, versus 76% in the control group (Lee and Kang 1994). Nevertheless, several experiments involving the addition of an extra nestling in swift species with a higher clutch size (2–3) (e.g., Perrins 1964; Bryant and Hails 1983; Tarburton 1987, 1990; Lee and Kang 1994) resulted in a range of nestling survival between 25–50% vs 58–96.5% in the control group. However the broad range of the results might be a sampling artifact, because sample size varied from two to 16 sets (ca 6–66 nestlings). The range of variation of nestling survival in two to three egg clutches (manipulated versus normal brood) is not as large as in one egg clutch species. Experiments on reducing the clutch size from two to one egg showed no major difference in survival or growth, in spite of the parents presumably having the capacity to provide extra food to the remaining nestling (Marín and Stiles 1992, Lee and Kang 1994).

Nestlings of many swift species store fat, and the fat storage capacity of the nestling might influence the upper mass limit during growth. If no major difference in growth occurs when brood size is reduced from two to one, the upper mass limit is probably imposed by food assimilation. The two one-egg clutch cypseloidines for which I have data, *C. cryptus* and *C. cherriei,* are tropical, non-migratory species, and they do not accumulate as much fat as *C. niger*. The maximum mass attained by nestlings of *C. cryptus* was 118.4% and *C. cherrie* was 111.7% of adult mass (Marín and Stiles 1992 and Marín, unpubl. data). While the maximum mass attained by *C. niger* nestlings was 148% of adult mass. The large quantities of fat accumulated by Common Swift (*Apus apus*) nestlings in England has been interpreted as an insurance against variable feeding and weather conditions (Lack and Lack 1951). However, for the Black Swift, this interpretation *per se* seems unsatisfactory, because weather conditions during the summer differ between England and the western United States, with far more rain in the former. Regardless, Lack's "insurance" hypoth-

esis against unpredictable food supplies should apply to all aerial feeders, although in different degrees. An additional factor that should be considered to explain energy storage is that nestlings of both species become independent from the parents for food as soon as they fledge. Furthermore, in both *A. apus* and *C. niger*, nestlings fledged early in the morning and none came back to roost at the nesting site, presumably they had migrated (Lack and Lack 1952, this study). At least in the Black Swift there seems to be a lower mass limit to fledging, which is still ca 113% of adult mass (see above); thus the extra stored energy would be needed for the first few days of independence or possibly as a "starter" supply of energy for the presumed migration. If migration occurs immediately, the storage of energy for migration while in the nest would be more efficient than waiting a further period of time to store energy. In other migratory swift species, at least in the New World, e.g., Chimney Swift (*Chaetura pelagica*), the nestlings return to roost to their nesting site for a few days, and they do not accumulate as much fat (Fischer 1958). Furthermore, they stay in communal roosts for at least two months before departure to the south (Marín, unpubl. data). In the Black Swift, the nestlings grew fast for the first days, and size of the nestlings was 75% of adult size when they became thermally independent. This fast growth and high energy storage also probably allows the nestling to survive low ambient temperatures and become thermally independent as early as possible. This permits the parents to conduct longer food-gathering trips. Thus, fat storage in Black Swift nestlings probably serves several functions.

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USING EGGSHELL EVIDENCE TO DETERMINE NEST FATE OF SHOREBIRDS

TODD J. MABEE[1]

ABSTRACT.—I collected eggshell evidence at nest sites of Piping Plover (*Charadrius melodus*), Snowy Plover (*C. alexandrinus*), and Killdeer (*C. vociferus*) in southeastern Colorado during 1994–1995, and determined nest fate independently. Successful nests of all three species generally contained eggshell fragments (ca 1–4 mm) in the scrape and eggshell membranes separated from the eggshell. In comparison, eggshell "tops" or "bottoms" were found only near successful nests of Piping Plovers and Snowy Plovers. I used discriminant function analysis to predict the probability of correctly classifying a nest's fate given different types of eggshell evidence. The use of eggshell fragment evidence resulted in the correct classification of the fate of Snowy Plover and Killdeer nests in 90% and 96% of the cases, respectively. Eggshell evidence can be used in future studies to determine nest fate of shorebirds and increase the precision of estimates of reproductive success. *Received 14 April 1996, accepted 1 March 1997.*

Assessing nest fate of precocial species such as shorebirds is problematic because chicks leave the nest soon after hatching and shortly thereafter their parents may move them a considerable distance to feeding areas. Consequently, establishing rigorous standards for determining nest fate is critical to understanding the biology of these species. Several criteria exist for classifying successful nests of shorebirds, such as the presence of at least one chick in or near the nest (Haig and Oring 1988), small eggshell fragments in the scrape produced during hatching (Hill 1985, Page et al. 1985, Paton 1995), and the absence of predator sign at nests whose clutches were old enough to have hatched. Conversely, failed nests have been classified by the absence of chicks and eggshell fragments and the presence of predator sign at nests too early in incubation to have hatched (Page et al. 1985, Paton 1995). Hill (1985) used the above criteria except for the absence of eggshell fragments.

The lack of a standard basis for determining nest fate can bias estimates of nest success and make comparisons among studies difficult. Two methods are used commonly to estimate reproductive success, and their precision depends on the accurate determination of nest fate. Observed nest success (the proportion of successful nests to total number of nests) utilizes only known-fate nests and, therefore, its accuracy is sensitive to the number and fate of unknown-fate nests removed from the analysis. By contrast, the Mayfield method (Mayfield 1961, 1975) utilizes unknown-fate nests in the analysis but the estimated daily survival rate is inflated

[1] Dept. of Biology, Colorado State Univ., Fort Collins, Colorado 80523.

by the number of unknown-fate nests. For both methods, the classification of unknown-fate nests would increase the precision of the estimate of reproductive success.

To date, no study has examined in detail the characteristics of successful or failed nests of shorebirds and the reliability of these characters in determining the fate of nests. My objectives here are to (1) describe the types of eggshell evidence collected at nests of three plover species in Colorado and (2) assess the utility of eggshell evidence in classifying nests as successful or failed.

STUDY AREA AND METHODS

I collected eggshell evidence at nest sites of Piping Plover (*Charadrius melodus*), Snowy Plover (*C. alexandrinus*), and Killdeer (*C. vociferus*) during the summers of 1994–1995 in southeastern Colorado as part of a research project that tested the effectiveness of predator exclosures on nesting success of plovers (Mabee and Estelle, unpubl. data). Study sites (reservoirs, altered and unaltered playa lakes) and water levels varied among years. In 1995, I floated eggs in tap water twice during incubation (mean = 12 d apart) to estimate the age of a clutch and to predict its hatching date. This technique has been used widely without reducing nest success (Hill 1985, Alberico 1995). Causes of nest failure included snakes, rodents, coyote (*Canis latrans*), raccoon (*Procyon lotor*), domestic dog (*Canis familiaris*), Great Blue Heron (*Ardea herodias*), Black-billed Magpie (*Pica pica*), cattle trampling, and inclement weather.

During both years, I searched at least a 10-m radius around a nest when it became inactive (either hatched or failed) and looked for eggshell tops, bottoms, or pieces. I also inspected the nest for the presence of eggshell fragments that are produced during pipping. I defined *eggshell tops* or *eggshell bottoms* as those parts of an eggshell that exhibited a nearly equidistant length from the center of the top or bottom eggshell to the broken edge of the shell and *eggshell pieces* as any part larger than 4 mm in length that did not exhibit the shape of an eggshell top or bottom. I used the term *eggshell fragments* to refer to parts that ranged from ca 1 to 4 mm. When I found eggshell tops, bottoms, or pieces, I inspected the eggshell membrane to see if it was partially separated from the eggshell. Waterfowl eggs that hatch exhibit an eggshell membrane separated from the eggshell (Klett et al. 1986). I considered an eggshell membrane to be separated from an eggshell if it was separated from the broken edge of the eggshell and if I could peel part of the membrane away from the eggshell.

Determining nest fate.—Determination of nest fate was independent of eggshell evidence. I classified failed nests only in 1995 because I did not float eggs in 1994. I classified a nest as successful when I observed at least one chick in or near a scrape and as failed when a clutch of eggs disappeared too early in incubation to have hatched (based on egg flotation) or when an entire clutch was abandoned. I assumed an average incubation period of 27 d for Piping Plovers (Haig 1992), 27.4 d for Snowy Plovers (Warriner et al. 1986, this study unpubl. data), and 26 d for Killdeers (Powers 1978) and considered any clutch <23 d, <23.4 d, or <22 d of age, respectively, to have failed.

Statistical analyses.—I used linear discriminant function analysis (Minitab 10.5 Xtra) to calculate the probability of correctly classifying the fate of a nest given the different types of eggshell evidence collected in 1995. I also ran a cross-validation procedure that omitted the first observation from the data set, developed a classification function using the remaining observations, and then classified the omitted observation. This iterative procedure was

TABLE 1

EGGSHELL EVIDENCE FOUND NEAR SUCCESSFUL AND FAILED NESTS OF PIPING PLOVER, SNOWY PLOVER, AND KILLDEER DURING 1994–1995. VALUES REPRESENT PERCENT OF TOTAL NESTS FOR EACH TYPE OF EGGSHELL EVIDENCE

Species	N	Eggshell fragments in scrape			Eggshell parts			Eggshell membrane		
		Present	Absent	Unknown[a]	None found	Piece	Top or bottom	None found	Separated	Attached
Successful–1994[b]										
Piping Plover	6	83	0	17	0	0	100	0	83	17
Snowy Plover	15	73	7	20	40	7	53	40	53	7
Killdeer	5	100	0	0	60	40	0	60	40	0
Successful–1995[c]										
Snowy Plover	10	100	0	0	30	10	60	30	70	0
Killdeer	6	100	0	0	100	0	0	100	0	0
Failed–1995										
Piping Plover	5	20	60	20	40	60	0	40	0	60
Snowy Plover	9	22	78	0	56	44	0	56	0	44
Killdeer	20	5	95	0	75	25	0	75	0	25

[a] Represents nests that were not searched for eggshell fragments.
[b] Unable to classify nests as failed due to lack of egg flotation data.
[c] No Piping Plover data available because all Piping Plover nests failed in 1995.

performed on all observations. Cross validation produced a less biased value because it removed bias due to observations having a large influence. All values presented were obtained from the cross-validation procedure. In cases where I found eggshell tops or bottoms and eggshell pieces at a nest site, I used eggshell tops or bottoms in the analysis because they provided the strongest indication of a nest's fate.

RESULTS

Eggshell evidence found near nests.—In 1994, most successful nests of Piping Plovers and Snowy Plovers and all successful nests of Killdeers contained eggshell fragments in the scrape (Table 1). All eggshell pieces and most eggshell tops or bottoms found near successful nests of Piping Plovers (5 of 6) and Snowy Plovers (7 of 8) contained an eggshell membrane that had separated from the eggshell, whereas no eggshell tops or bottoms were found in the vicinity of successful Killdeer nests.

In 1995, all successful nests of Snowy Plovers and Killdeers contained eggshell fragments in the scrape. Eggshell pieces and tops or bottoms found near successful nests of Snowy Plovers always contained an eggshell membrane that had partially separated from the eggshell. As in 1994, no eggshell tops or bottoms were found near successful Killdeer nests (Table 1). Because all Piping Plover nests failed in 1995 due to weather,

TABLE 2

EGGSHELL EVIDENCE AND ITS PROBABILITY OF CORRECTLY CLASSIFYING SNOWY PLOVER AND KILLDEER NESTS DURING 1995 USING LINEAR DISCRIMINANT FUNCTION ANALYSIS

Eggshell evidence	Successful nest	Failed nest	Oveall nest fate[a]
Snowy Plover			
Eggshell fragments	100	78	90
Eggshell parts	60	100	79
Eggshell membrane	70	100	84
Fragments and parts	90	78	84
Fragments and membrane	100	78	90
Killdeer			
Eggshell fragments	100	95	96

[a] Overall nest fate is the probability of correctly classifying a nest as successful or failed.

predation, or humans, I could not classify eggshell evidence for successful nests.

In 1995, most failed nests of Piping Plovers, Snowy Plovers, and Killdeers did not contain eggshell fragments in the scrape (Table 1). However, eggshell fragments were found in one Piping Plover nest that failed due to hail, in Snowy Plover nests that failed due to a rodent (N = 1) and an unknown predator (N = 1), and in one Killdeer nest that failed due to an unknown predator. All eggshell pieces found near failed nests contained attached eggshell membranes, however, no eggshell tops or bottoms were found near failed nests.

Classification of nest fate.—In general, results from the linear discriminant function analysis corroborated the patterns exhibited in the descriptive summary of eggshell evidence. To assess the strengths and biases of the various types of eggshell evidence (predictors) in classifying nest fate, one needs to examine the probability of correctly and incorrectly classifying nest fate. For example, presence or absence of eggshell fragments in Snowy Plover nests correctly classified 100% of successful nests and 78% of failed nests (Table 2). Therefore eggshell fragments overestimated nest success by incorrectly classifying 22% of failed nests as successful nests. To compare the overall ability of predictors to classify nest fate correctly, it is necessary to examine *overall nest fate*, the probability of correctly classifying a nest as successful or failed (Table 2).

For Snowy Plovers, eggshell fragments were the best predictor of successful nests, whereas eggshell parts (tops, bottoms, or pieces) and eggshell membrane were the best predictor of failed nests. Eggshell fragments or the combination of eggshell fragments and eggshell membrane clas-

sified overall nest fate with equal strength (Table 2). Multiple predictors such as eggshell parts, eggshell membrane, or the combination of eggshell fragments with these predictors could not be used to classify nest fate of Snowy Plovers or Killdeers because they were highly intercorrelated.

Eggshell fragments were the single best predictor of both successful and failed nests, and overall nest fate of Killdeers (Table 2). Because eggshell parts were not found near successful Killdeer nests, neither eggshell parts, eggshell membrane, nor combinations of these predictors with eggshell fragments could be evaluated for successful Killdeer nests. Unsuccessful Killdeer nests were classified correctly only 25% of the time by either eggshell parts or eggshell membrane. I could not analyze Piping Plover eggshell evidence because there were no successful Piping Plover nests in 1995.

DISCUSSION

The accuracy of eggshell evidence, particularly eggshell fragments, in classifying nest fate for plovers is demonstrated clearly by both descriptive evidence and linear discriminant function analysis. I found eggshell fragments in 88% of successful nests and in only 12% of failed nests of all three species. Eggshell fragments are expected in successful nests because chicks break through the eggshell and produce small pipping fragments when hatching. Eggshell fragments should not be used to classify nest fate in species that reuse the same nest site, unless nest sites are seasonally obliterated by environmental conditions.

Eggshell tops or bottoms were also useful indicators of nest fate as they were found at 65% of successful nests and 0% of failed Piping Plover and Snowy Plover nests. It appears that chicks pip through an eggshell at a fairly uniform level around the top of the egg and produce well-defined shell tops and bottoms. Killdeer must have taken eggshell tops and bottoms >10 m away from the nest, a behavior documented for other shorebirds (Sordahl 1994, Page et al. 1995).

Eggshell pieces >4 mm in length were found in both successful and failed nests and were not as useful in classifying nest fate as eggshell fragments or eggshell tops or bottoms. Pieces can be produced during a predation event or hail storm, or they may be part of a deteriorated eggshell top or bottom. Likewise, eggshell fragments may be produced by the same events, but it was usually possible to determine nest fate when predator sign, eggshells, clutch age, and recent weather were taken into consideration.

Eggshell membranes were also useful indicators of nest fate because they are tightly adhered to an eggshell early in incubation but separate as the embryo develops and resorbs calcium from the eggshell (Packard and

Clark 1996). During this study, depredated eggs of a young age contained transparent eggshell membranes that were tightly adhered to the eggshell, whereas eggshell tops or bottoms from successful nests contained white eggshell membranes that were partially separated from the eggshell.

The pattern of eggshell evidence exhibited near nests of the three plovers was consistent between years and among locations for each species. The high variability of study areas and of environmental conditions between years suggest that eggshell evidence may be used to classify nest fate for shorebirds in other locations. I recommend using eggshell evidence to supplement methods used to determine nest fate and to classify unknown-fate nests. The type of eggshell evidence that classifies nest fate most accurately may vary depending on the predator assemblage and location. If determining nest fate is critical, eggs must be floated to strengthen the determination of nest fate. In general, shorebird nests should be monitored at regular intervals (e.g., every 3–4 d) and immediately examined for eggshell evidence in the nest and within at least a 10-m radius of the nest when it becomes inactive. If time to monitor nests is limited, I recommend using the presence or absence of eggshell fragments in the nest scrape to determine nest fate because it is the most objective piece of evidence gathered and is easy to obtain.

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SHORT COMMUNICATIONS

Comparison of breeding bird communities in bottomland hardwood forests of different successional stages.—The area of bottomland hardwood forests, an important habitat for many birds, is declining (Harris and O'Meara 1989, Hefner et al. 1994). From the mid-1970s to mid-1980s, forested wetlands in the southeast U.S. declined by 1.3 million ha (Hefner et al. 1994) and are expected to decrease into the year 2030 (USDA Forest Service 1988). An estimated 13.3 million ha of forested wetlands remain in the southeastern U.S. (Hefner et al. 1994). These forests are important for several species of birds, particularly Neotropical migrants with diminishing populations. However, bottomlands in different successional stages have different habitat qualities. Late-successional habitats exhibit greater vegetative diversity, including multiple vegetation layers, high vegetation density, edges, snags, and interspersion of habitats (Bull and Skovlin 1982) which provide more potential nesting and foraging sites. Bird density and species diversity parallel structural diversity in riparian habitats (Swift et al. 1984) and generally are greatest in late-successional habitats such as mature bottomland forests (Zimmerman and Tatschl 1975, Dickson 1978). We compared avian abundance, species richness, and species diversity among bottomland hardwood forests of three successional stages.

Study area and methods.—We conducted this study on the U.S. Dept. of Energy's Savannah River Site (SRS). This 78,000-ha facility in Aiken, Allendale, and Barnwell counties, South Carolina, is composed of pine stands of various ages in the uplands and bottomland hardwoods associated with the numerous creeks that traverse the site. Study plots were located in three bottomland corridors, representing early-, mid-, and late-successional bottomland hardwood forests, respectively. Pen Branch, an early-successional bottomland corridor, received regular influxes of thermal effluent from the SRS's K Reactor beginning in 1954. The original bottomland hardwood vegetation was destroyed by elevated water levels and sediment loads, and water temperatures in excess of 45°C (Sharitz et al. 1974). Thermal input ceased in 1988, but high flow rates continued until August 1993. The creek currently is dominated by black willow (*Salix nigra*) and smooth alder (*Alnus serrulata*), interspersed with grassy openings. The mid-successional bottomland, Steel Creek, received thermal effluent until 1968 when the last reactor on the creek was closed. It is dominated by large black willow and smooth alder. Red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and sycamore (*Platanus occidentalis*) also are present. The late-successional bottomland, Tinker Creek, never received thermal effluent. Timber harvest and other disturbances in the creek have been minimal for over 60 years (Workman and McLeod 1990). Swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple, and tulip poplar (*Liriodendron tulipifera*) dominate the overstory. Midstory species include red maple, American holly (*Ilex opaca*), sweetbay (*Magnolia virginiana*), and wax myrtle (*Myrica cerifera*).

In each corridor, we sampled 12 randomly located habitat plots. Percent green ground cover, percent water cover, shrub density, canopy height, percent canopy closure, and basal area were measured according to James and Shugart (1970). Vegetative profile was estimated using a 3-m density board (Nudds 1977). Estimated avian community parameters were correlated with habitat variables using Pearson's correlation coefficient. Avian censuses were conducted along each creek five times per year from mid-May to late June, 1994–1995. The fixed-radius (50 m) point count method (Ralph et al. 1993) was used to estimate avian abundance, species richness, and species diversity. Six census points were located at least 50 m from the edge of each bottomland and were separated by 200 m. Censusing began at

TABLE 1

VEGETATIVE CHARACTERISTICS OF THE THREE BOTTOMLANDS SURVEYED ON THE SAVANNAH RIVER SITE, 1994–1995

	Pen Branch	Steel Creek	Tinker Creek
Years since disturbance	7	27	60+
Canopy height (m)	8.3 ± 0.9	12.2 ± 0.8	18.3 ± 0.8
Canopy closure (%)	52.3 ± 5.4	83.4 ± 2.6	92.5 ± 0.8
Green ground cover (%)	61.7 ± 4.3	46.3 ± 4.9	36.0 ± 4.1
Water cover (%)	17.3 ± 2.7	9.6 ± 2.3	35.8 ± 6.4
Shrubs per ha ($\times 10^3$)	119.0 ± 0.4	159.0 ± 1.2	139.0 ± 1.3
Basal area (m^2 ha^{-1})	8.0	20.6	43.7
Basal area by species (%)			
Salix nigra	76.3	33.6	0.0
Alnus serrulata	3.3	19.1	2.5
Acer rubrum	1.7	12.0	17.4
Liquidambar styraciflua	0.0	19.4	4.8
Liriodendron tulipifera	0.0	0.0	7.6
Nyssa sylvatica var. *biflora*	0.0	1.0	49.9

sunrise and was completed within 3.5 h. All visual and auditory detections of birds, except those flying over the site, were recorded for 5 min. Species detected ±3 min of each point count period while en route to census points and species detected outside the census plot were recorded for inclusion in the species list for each site. No censusing was done during high wind or rain.

Abundance is reported as mean number of birds per census point. Species richness is mean number of species per creek. Bird species diversity, reported as mean diversity per creek, was computed using the Shannon-Weaver formula (Shannon and Weaver 1949). Among creeks, comparisons of avian abundance by habitat preference and migratory strategy (Whitcomb et al. 1981), species richness, and diversity were tested with one-way analysis of variance and Tukey's test was used to compare means for differences ($\alpha = 0.05$). Comparisons within species among sites were made if sample sizes were large ($N \geq 30$).

Results.—There were pronounced differences in the vegetation among the three bottomlands (Table 1). As expected, canopy height, canopy closure, and basal area, increased with age of the stand. The early-successional site was dominated by black willow and smooth alder of relatively uniform height. Early-successional shrubs, including wax myrtle and buttonbush (*Cephalanthus occidentalis*), were common. The mid-successional bottomland was a mix of large black willow and smooth alder and some later successional species.

Avian abundance was negatively correlated with canopy closure ($r = -0.25$, $P = 0.02$). Richness was negatively correlated with ground cover ($r = -0.56$, $P = 0.02$) and coverage of the two lower sections of the profile board ($r = -0.69$, $P = 0.001$; $r = -0.59$, $P = 0.01$) and positively correlated with canopy height ($r = 0.57$, $P = 0.01$), canopy closure ($r = 0.63$, $P = 0.01$), and basal area ($r = 0.70$, $P = 0.001$). There were no significant differences in abundance, richness, or diversity within treatments between years, so data were pooled. Avian abundance was greater in the early-successional bottomland than in the mid-successional bottomland (Table 2). Species richness increased as successional stage increased among the three bottomlands. Diversity was greater in the late-successional creek

TABLE 2

MEAN ABUNDANCE, RICHNESS, AND DIVERSITY OF BIRD SPECIES IN BOTTOMLAND HARDWOOD FORESTS IN DIFFERENT STAGES OF SUCCESSION ON THE SAVANNAH RIVER SITE, 1994–1995

	Abundance		Richness		Diversity[a]	
Site	Mean	SE	Mean	SE	Mean	SE
Pen Branch	5.08	0.23 A[b]	11.6	0.5 C	1.89	0.05 B
Steel Creek	3.72	0.25 B	16.3	0.6 B	2.11	0.07 AB
Tinker Creek	4.20	0.37 AB	19.1	0.8 A	2.34	0.09 A

[a] Bird species diversity computed using information theory formula: $-\Sigma p_i \log_e p_i$.
[b] Means followed by the same letter, within the same column, are not significantly different at $\alpha = 0.05$ (Tukey's Studentized Range Test).

compared to the early-successional. Forest interior species were most common in the late-successional bottomland (Table 3). The early-successional creek contained more forest edge/scrub species than the other creeks. No forest edge/scrub species were recorded in the late-successional creek over the two years. Abundance of forest interior/edge species and field/edge species did not differ among the creeks.

Short-distance migrants, defined as species that move a few hundred km to wintering grounds (Whitcomb et al. 1981), were more than twice as abundant in the early-successional creek than in the other creeks (Table 3). Several Neotropical migrant species were detected in Pen Branch, including Ruby-throated Hummingbird (*Archilochus colubris*), Yellow-billed Cuckoo (*Coccyzus americanus*), Red-eyed Vireo (*Vireo olivaceus*), Northern Parula (*Parula americana*), Hooded Warbler (*Wilsonia citrina*), and Indigo Bunting (*Passerina cyanea*). Two species were found only in Pen Branch, Yellow-breasted Chat (*Icteria virens*) and Blue

TABLE 3

MEAN ABUNDANCE BY HABITAT CATEGORY AND MIGRATION CATEGORY OF BIRD SPECIES IN EARLY- (PEN BRANCH), MID- (STEEL CREEK), AND LATE-SUCCESSIONAL (TINKER CREEK) BOTTOMLAND HARDWOOD FORESTS ON THE SAVANNAH RIVER SITE, 1994–1995

	Pen Branch		Steel Creek		Tinker Creek	
	Mean	SE	Mean	SE	Mean	SE
Habitat category[a]						
Interior	0.3	0.5 B[b]	0.6	0.2 B	5.5	0.5 A
Interior/edge	21.5	1.2 A	19.8	1.8 A	18.9	1.4 A
Edge/scrub	6.2	1.1 A	0.3	0.2 B	0.0	0.0 B
Field/edge	2.2	0.5 A	1.1	0.3 A	0.8	0.4 A
Migration category						
Resident	3.3	0.8 A	5.9	1.1 A	3.9	0.7 A
Short-distance	17.4	1.3 A	7.6	0.9 B	7.4	1.0 B
Neotropical migrant	9.5	1.5 B	8.3	0.9 B	13.5	0.7 A

[a] Habitat and migration categories after Whitcomb et al. (1981).
[b] Means followed by the same letter, within the same row, are not significantly different at $\alpha = 0.05$ (Tukey's Studentized Range Test).

Grosbeak (*Guiraca caerulea*). Of these species, only the Northern Parula had a sample size large enough to compare among sites, and its abundance was not different among the three creeks. However, the Hooded Warbler, Northern Parula, Red-eyed Virco, and Yellow-billed Cuckoo generally were detected more often in the late-successional creek and in similar numbers in the mid-successional creek compared to the early-successional creek.

The abundance of Neotropical migrants was greatest in the late-successional site. Swainson's Warbler (*Limnothlypis swainsonii*), Summer Tanager (*Piranga rubra*), and Eastern Wood-Pewee (*Contopus virens*) were found only in the late-successional creek, and Acadian Flycatcher (*Empidonax virescens*), Louisiana Waterthrush (*Seiurus motacilla*), and Wood Thrush (*Hylocichla mustelina*) were found almost exclusively in that site. The American Crow (*Corvus brachyrhynchos*) and Brown-headed Nuthatch (*Sitta pusilla*) also were found only in Tinker Creek. Prothonotary Warblers (*Protonotaria citrea*) were equally abundant in the mid- and late-successional bottomlands but were not seen in Pen Branch. The mid- and late-successional creeks contained similar numbers of the three woodpecker species detected: Pileated (*Dryocopus pileatus*), Red-bellied (*Melanerpes carolinus*), and Downy (*Picoides pubescens*). In the early-successional creek, only the Downy Woodpecker was observed.

Discussion.—Most researchers who have related avian community parameters to forest successional stage have reported increasing abundance, species richness, and diversity with increasing successional stage (Karr 1968). However, Shugart and James (1973) reported a drop in richness and diversity at the "climax" stage. In our study, richness and diversity values were comparable to previous studies (Karr 1968, Zimmerman and Tatschl 1975), although there was no drop in either value in the late-successional creek. Zimmerman and Tatschl (1975) observed greater breeding bird abundance but lower richness and diversity in a young forest than in a mature hardwood stand in a Kansas floodplain. Similarly, our early-successional creek had greater avian abundance than the other creeks, significantly greater than the mid-successional bottomland. Richness and diversity generally were greater in the two later successional bottomlands. The greater abundance in Pen Branch compared to Steel Creek was unexpected because avian density and species diversity usually parallel structural diversity (Swift et al. 1984). Pen Branch was characterized by three habitat types: short willow/alder, herbaceous cover 2–3 m high, and patchy grassy openings. Steel Creek, the mid-successional bottomland, appeared to have a greater degree of vegetative heterogeneity than Pen Branch, and this can be inferred by its greater canopy height, more shrubs per ha, greater basal area, and greater variety of tree species compared to Pen Branch. Nonetheless, Steel Creek had the lowest abundance of birds among the creeks.

The change in community composition was well-defined. Late-successional bottomlands generally contain a high variety and abundance of Neotropical migratory species (Karr 1968), some of which are almost solely associated with this habitat type (Dickson 1991). In our study, the late-seral stage contained a greater abundance of Neotropical migrants and forest interior birds than the other two sites. Most species in Tinker Creek were either forest interior or forest interior/edge species. The high abundance of short-distance migrants in the early-successional bottomland largely is the result of the creek being dominated by a few short-distance migratory species. Common Yellowthroats (*Geothlypis trichas*), White-eyed Vireos (*Vireo griseus*), and Red-winged Blackbirds (*Agelaius phoeniceus*), plus one Neotropical migrant, the Indigo Bunting, comprised 70% of the birds detected in Pen Branch and contributed to the low diversity value. As a group, these four species were more abundant ($P < 0.05$) in Pen Branch than in the other creeks. Although not significant, Steel Creek contained the greatest number of resident birds, primarily Northern Cardinals (*Cardinalis cardinalis*).

Results of this study emphasize the importance of mature bottomlands as habitat for a number of interior Neotropical migrant species. Similar results have been reported for bottomland habitats elsewhere in the southeastern U.S. (Hamel 1989, Harris 1989) and other

regions of the country (Knopf et al. 1988). Maintenance of these habitats is important because the populations of many interior species and Neotropical migrants likely are declining. These results also demonstrate the changes in the avian community along a successional gradient. Maximizing avian species composition may require maintenance of a diversity of habitat types and successional stages. This will require proper design and management of forested bottomlands to secure the future for species currently losing habitat.

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The first nest records of the Sooty Antbird (*Myrmeciza fortis*) with notes on eggs and nestling development.—The Neotropical bird family Thamnophilidae (sensu Sibley and Alquist 1990, Sibley and Monroe 1990) is large yet relatively poorly known (Monroe and Sibley 1993, Ridgely and Tudor 1994). Nests, eggs, and young of most species are unknown. Here we describe for the first time the nests, eggs, and nestlings of the Sooty Antbird (*Myrmeciza fortis*) from a site in southeastern Peru. We also compare the nests of this species to previously described nests of *Myrmeciza* spp. and to other species in the Thamnophilidae.

Methods.—Two nests were discovered during the late dry season in a mature floodplain forest near Cocha Cashu Biological Station, Manu National Park, Department of Madre de Dios, Peru. The habitat is described in Terborgh et al. (1984). The first nest was found in 1991 by URS, and the second in 1994 by FAW.

Data were recorded for the eggs of nest 1 only. Development was recorded only for nestlings in nest 2 in which data were taken each day (except one) between 13:30 and 15:00 from day 1 until fledging. The nestlings were marked with a black marking pen each day until they were color banded on day 8. In addition, they were weighed with a Pesola spring balance to the nearest 0.1 g, and the wing chord, tail, and bill length of each were measured to the nearest 1 mm, with a wing ruler.

Nest placement and description.—Both nests were concealed in leaf litter on the forest floor at the edge of frequently traveled trails. Nest 1 (Figs. 1, 2) was in a small mound of leaf litter (25 cm high, 30 cm in diameter) between low buttresses of a mid-canopy tree; nest 2 was located in a small mound of leaf litter (50 cm high, 27 cm in diameter) whose surface sloped up from the ground at a 45° angle. Each nest consisted of a spherical chamber with a short horizontal entrance tunnel. The floor of the spherical chamber was sunk slightly lower than the level of the entrance tunnel. The horizontal roof was in a single plane to the forest floor (Fig. 1). The dimensions of the entrance tunnels were: Nest 1—ca 2–3 cm deep, 4 cm high, 5 cm wide and Nest 2—ca. 3.6 cm deep, 3.4 cm high, 3.6 cm wide. Nest 1 had

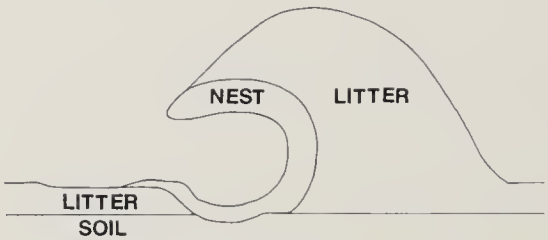

FIG. 1. Lateral cross section of a Sooty Antbird nest.

a short runway leading to the entrance tunnel. The dimensions of the spherical chambers were: Nest 1—6–7 cm in diameter and Nest 2—ca 5.2 cm deep, 3.8 cm high, 4 cm wide.

The exterior rim of the entrance tunnel of nest 2 was comprised of strips of tightly woven plant material ranging from 3.6 to 18.8 cm long and was cushioned with tiny pieces of leaves. The interior chambers of both nests were neatly lined with interwoven plant fibers, either thin strips torn from the margins of palm leaves and grass blades or the thread-like "reins" that are shed from the pinnae (leaflets) of new palm leaves; some fibers were still green. Plant matter forming the spherical chamber of nest 2 measured ca 0.8–6.0 cm long and 0.1–0.6 cm wide.

FIG. 2. Eggs in nest 1.

FIG. 3. Nestlings in nest 2 at day 8.

Results.—When found both nests contained two eggs. The eggs of nest 1 were pyriform to long-pyriform with a smooth matte or very slightly glossy finish. They were creamy-white with dark brown or maroon scrawls concentrated toward the blunt end (Fig. 2). Eggs of nest 1 were revealed when an adult female was flushed from the nest on 23 September (day 1). Eggs were also observed on days 2 and 3. On days 3, 4, and 6 an adult male was seen on the nest. On day 10 (2 October) the nest was empty but undisturbed. Nest 2 was discovered on 1 October when an adult male was flushed from the nest, which contained two eggs. An adult female was noted on the nest each day thereafter until nestlings appeared on 11 October.

On day 1 (11 Oct.) the nest contained two purplish blue nestlings lacking down but with pin feathers in spinal and caudal tracts: Their eyes were closed. They had a yellow gape and were making faint peeping sounds. On day 2 nestling A had pin feather development in scapular region, the gape color was fading; nestling B was making faint peeping sounds. Both nestlings had broken sheaths along the spinal tract. On day 3 there were additional feathers in spinal and scapular regions, some with broken sheaths. Nestling A had ventral pin feathers and its gape color continued to fade. Nestling B had capital tract pin feathers. On day 5 there were pin feathers in the capital, spinal, and caudal regions and the nestlings' eyes were beginning to open. Nestling A was standing and spreading its wings. On day 6, nestlings' eyes were fully open: Broken sheaths exposed black feathers in all areas except on the tail (nestlings A and B) and on the crown (nestling A). Nestling A aggressively pecked at FAW's hands while being measured. Nestling B's gape was still yellow. On day 7 nestling B had fully developed crown feathers. On day 8 there were white tips on bill, brown primaries were developing, and there were bare patches around eyes. Nestling A was observant. Its gape color was nearly gone and its crown feathers were fully developed (Fig. 3). On day 9 the nestlings were alert; few caudal pin feathers remain. Nestling A escaped and hopped down the trail. It was caught and returned to the nest, but was missing three hours later. Nestling B was still present 3 h later, lowering its

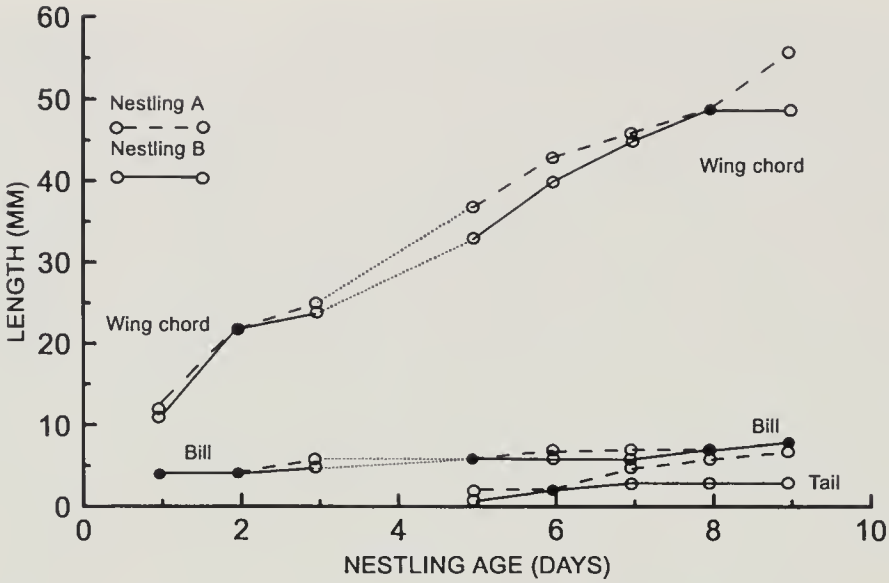

FIG. 4. Development in two Sooty Antbird nestlings. The dotted line indicates no data for day 4, and the solid dots represent equal values.

head and peeping. On day 10 the nest was empty and ripped from the leaf pile still intact. Nestling measurements are given in Fig. 4.

Discussion.—The minimum possible incubation period for nest 2 was 10 days, but the eggs may have been in the nest for several days before it was discovered. Incubation times reported for other Thamnophilidae range from 14–18 days (Skutch 1996). The male was observed on the nest only once. Since the nest was checked at approximately the same time each day, the male may have incubated at other times. This is likely the case with nest 1, in which the male was observed on the nest on days 3, 4, and 6, presumably incubating. As a general rule, the male and female alternate incubation bouts in the Thamnophilidae (Skutch 1996).

The nestling period for nest 2 was nine days, although the young may have fledged a day early because of handling by the investigator. This duration agrees with nestling periods reported for other Thamnophilidae which range from 9 to 15 days (Skutch 1996).

Antbird nests vary in structure and placement, ranging from simple, open cups or pensile pouches that are supported by forked branches to large, closed balls placed near or on the ground. Others are open cups set in cavities of tree trunks or in bunches of leaves among plants on the ground (Sick 1993). According to Skutch (1969), antbird nests are rarely found on the ground. Of the 19 *Myrmeciza* species (Monroe and Sibley 1993), the nests of only three other species, Chestnut-backed Antbird (*M. exsul*), Ferruginous-backed Antbird (*M. ferruginea*), and White-bellied Antbird (*M. longipes*), have clearly been described, while the nest of Goeldi's Antbird (*M. goeldii*), has been only briefly noted. *Myrmeciza exsul* places its loosely built, cup-shaped nests on short plants, dead palm leaves or debris near the ground (Skutch 1969, Wetmore 1972, Willis and Oniki 1972) or in small ferns and young palms at heights of 32.5–45.0 cm (egg/nest specimen data from the Western Foundation of Vertebrate Zoology). The open cup nests of *M. ferruginea* (Haverschmidt and Mees 1994) and *M. goeldii* (M. B. Robbins, pers. comm.) are placed on the ground, whereas the open cup nests of *M. longipes* are usually 1–2 m above the ground (Wetmore 1972).

In contrast, the two nests of *Myrmeciza fortis* described here were on or near the ground, domed, and concealed within mounds of leaf litter. This type of nest structure is relatively uncommon within the family, although similar nests are known in a few other antbird genera.

The "leafy ball" nest of the White-backed Fire-eye (*Pyriglena leuconota*) is set on or near the ground (Willis 1981) and is of similar design to the nest of the Ovenbird (*Seiurus aurocapillus*), as reported by Bond and Meyer de Schauensee in Stone (1928). The White-shouldered Fire-eye (*Pyriglena leucoptera*) (Euler 1867, Fraga and Narosky 1987, Skutch 1996) is also known to build an oven-shaped nest with a side entrance near or on the ground. An oven-shaped nest, possibly of the Slender Antbird (*Rhopornis ardesiaca*) has also been reported (Teixeira 1987). A similar nest has been described for the Brown-bellied Antwren (*Myrmotherula gutturalis*) (Oniki and Willis 1982) which is a notable exception to the above-ground open cup or pensile nests typical of many *Myrmotherula* species (Hilty and Brown 1986).

The systematic relationships of *Myrmeciza* species are poorly resolved, both within the genus (Zimmer 1932) and with respect to other genera (Ridgley and Tudor 1994). Differences among the nests of *Myrmeciza* species adds to the recorded heterogeneity of this genus (Ridgely and Tudor 1994, K. V. Rosenberg and M. J. Braun, unpubl. data). *Myrmeciza* clearly warrants further study. Additional information on the nests of other species may help to advance our understanding of the systematics and evolutionary history of this genus and of the Thamnophilidae.

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FIONA A. WILKINSON, *Biological Resources Division, United States Geological Survey, Room #378, National Museum of Natural History, 10th St. and Constitution Ave., NW, Washington, District of Colombia 20560-0111;* AND UNA R. SMITH, *Dept. of Biology, Yale Univ., New Haven, Connecticut 06520-8104.* *Received 15 Aug. 1996, accepted 26 Nov. 1996.*

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Intermittent incubation during egg laying in House Sparrows.—The clutch sizes of many passerine birds show considerable phenotypic plasticity (Perrins and Moss 1975, Hogstedt 1980, Pettifor et al. 1988), but the proximate mechanisms responsible for determining clutch size are poorly understood. Recent studies have suggested that the onset of incubation behavior, which commences gradually during egg laying in some species, may play a role in the proximate determination of clutch size (Haftorn 1981, Mead and Morton 1985, Meijer 1990, Haywood 1993). Anderson (1995) proposed that the mechanism of clutch size determination in the House Sparrow (*Passer domesticus*) involves (1) female condition at some point prior to the beginning of egg laying, establishing both a prospective clutch size and a corresponding schedule for the onset of incubation, (2) tactile feedback from the presence of at least one egg in the nest causing continuation of incubation behavior and resultant increases in prolactin secretion, and (3) rising prolactin levels suppressing follicular development causing egg production to cease at the predetermined number. This proposal would require that incubation begin early in the laying sequence, such as has been observed in several other passerines (Haftorn 1981, Zerba and Morton 1983, Meijer 1990, Hebert and Sealy 1992).

Little is known about the onset of incubation in the House Sparrow. Asynchronous hatching occurs in House Sparrow broods (Veiga and Vinuela 1993, Anderson 1994), which suggests that incubation begins prior to the completion of egg laying. It is also known that female House Sparrows roost in the nest on the eggs during egg laying (Summers-Smith 1963) and spend more time on the nest during the day as egg laying progresses (Summers-Smith 1963, North 1980), but it is not known if heat is being applied to the eggs during these periods. A gradual onset of incubation behavior involving intermittent bouts of incubation early in the laying sequence would be required for the mechanism proposed above, while an abrupt onset late in the egg laying cycle would be inconsistent with it. The purpose of this preliminary study was to determine if such intermittent bouts of incubation occur during egg laying in the House Sparrow.

TABLE 1

DATE OF INITIATION, CLUTCH SIZE AND APPARENT TIME OF EGG LAYING FOR SIX CLUTCHES IN WHICH NEST CUP TEMPERATURES WERE MONITORED DURING THE LAYING PERIOD

Nest-box number	Date of initiation	Clutch size	N	Time of egg laying	
				Range	Mean (SD)
256.1	7/6	6	3	6:55–7:00	6:58 (:03)
256.2	7/23	5	5	6:51–7:11	7:03 (:08)
266	7/23	2	1	7:50	—
209	7/24	4	4	6:50–7:05	6:59 (:06)
251	7/29	5	4	6:30–7:05	6:54 (:16)
284	7/30	4	4	6:30–7:05	6:51 (:15)

Study area and methods.—The study was conducted at a dairy farm near the Univ. of Michigan Biological Station (UMBS), Cheboygan County, Michigan (45°34′N, 84°40′W), from 7 July to 7 August 1995. Six nest boxes located on the inside south wall of an open shed housing dairy cattle were used for the experiment. Nest boxes were visited daily, usually between 07:30 and 09:00 EDT, to check nest contents.

Thermocouple thermometers (20 gauge, type T) were placed in the floor of the nest cup in four nest boxes (three in which egg laying was occurring) during the late afternoon of 7 July. The thermocouples were connected to an OWL/HOOT on-site weather logger (eme systems, 2229 Fifth St., Berkeley, CA 94710). Temperatures were recorded at five-minute intervals, which required downloading of the temperature records every three days, and the weather logger was taken to UMBS at two- or three-day intervals for downloading. This process resulted in a disruption of data collection for approximately one hour, usually around 09:30 EDT. Data for a three-day period (12–15 July) were lost in the downloading process, and data from one 24-h period (9–10 July) were not recorded due to a wiring error.

Two of the laying females abandoned their nests, apparently due to the extensive disturbance during the two hours required to set up the equipment, while the third (256.1) continued to lay. Following the loss of data in downloading mentioned above, the nest contents of four nest boxes were removed on 18 and 19 July to stimulate renesting (see Anderson 1979). Thermocouples were moved occasionally to other nest boxes as nest building or clutch initiation in those boxes occurred. Females were captured and banded during incubation following the completion of their clutches.

One thermocouple was constantly maintained in an inactive nest box to provide continuous data on ambient nest cup temperature (T_a). Different nest boxes served as the control at different times due to changes in occupancy during the study. Nest cup temperatures in occupied nest boxes (T_n) were compared to T_a. Incubation was inferred from sharp rises in T_n in occupied nests or by continuous maintenance of T_n well above T_a. It might be argued that elevated T_n was simply due to radiative heat from the presence of an adult in the nest. The lack of a difference between T_n and T_a during many of the nights during egg laying in several of the nests (see below) when the female was presumably roosting on the eggs (cf Summers-Smith 1963) suggests that the sharp rises in T_n instead represent application of heat from the brood patch of the female. Male House Sparrows do not develop brood patches (Summers-Smith 1963, Anderson, pers. obs.) and, therefore, do not truly incubate.

A sharp rise in the difference betwen T_n and T_a between 06:00 and 07:30 EDT (shortly after sunrise) on each day during the egg-laying period was presumed to coincide with egg

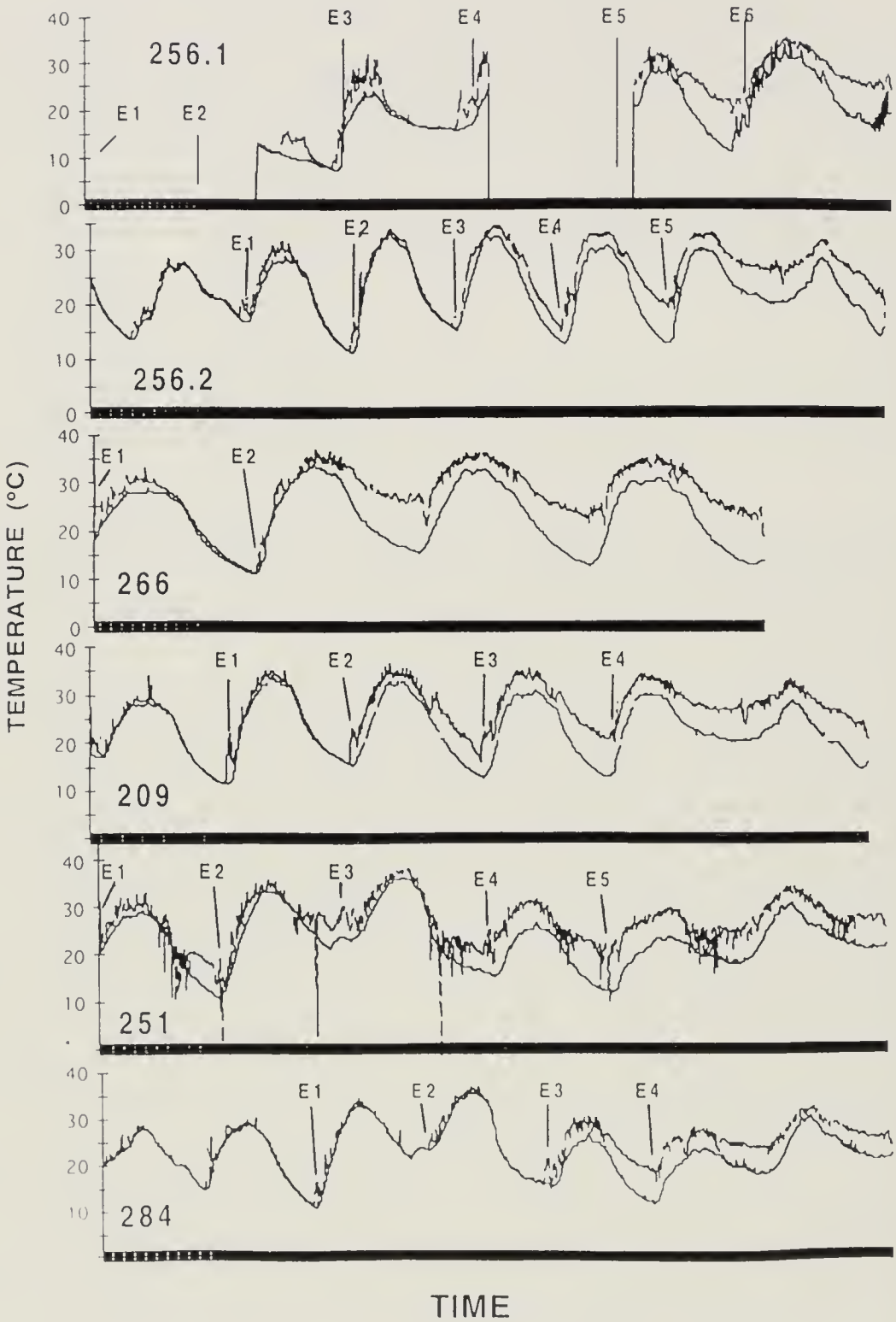

FIG. 1. Traces of nest cup temperatures during egg laying in six House Sparrow nests in northern lower Michigan, July–August 1995. Lower trace in each sequence is ambient temperature in the nest cup of an unoccupied nest box, with the sinusoidal shape representing daily fluctuations in ambient temperature, with the low point in each trough occurring approximately at dawn (about 07:00 EDT). Approximate times of egg laying in the occupied nest-boxes are designated by E1, E2, etc., for first, second, and subsequent eggs in the clutch.

laying, which normally occurs near dawn in the House Sparrow (Summers-Smith 1963, Anderson, pers. obs.). The time of the peak difference between T_n and T_a during this period was interpreted as the actual time of egg laying.

Results and discussion.—Temperature records were obtained for the entire laying sequence for five clutches (256.2, 266, 209, 251, and 284) and for a part of the laying sequence for one clutch (256.1) (Table 1). Anomalous temperature readings occurred at intermittent intervals in nest box 251, probably due to a damaged lead, but the basic pattern of incubation onset was still discernible. The same female laid both clutches in nest box 256 (256.1 and 256.2), while the female laying the abnormally small two-egg clutch (see Anderson 1994) had been captured in the same nest box on 17 July on the 15th day of incubation of a clutch of infertile eggs. The laying histories of the three other females were not known.

Table 1 also contains data on the apparent time of egg laying in the six nests. Egg laying occurred about 45 minutes after sunrise (N = 21, mean = 44.9 min, SD = 18.9).

Fig. 1 shows the temperature traces for the six clutches. Each trace shows T_n compared to T_a for the same interval. Haftorn (1981) distinguished between incubation *sensu stricto*, any application of heat to the eggs, and the beginning of continuous incubation, the time when the female begins continuous attentiveness to the eggs. Incubation *sensu stricto* began in all six clutches prior to the laying of the last egg. In the five nests for which complete temperature records for the entire laying period are available, all five showed periods of daytime incubation beginning with the day of the laying of the first egg. The intensity and duration of these periods varied among nests (Fig. 1), and, in general, appeared to increase with subsequent days. Some periods of nocturnal incubation were also evident (after the laying of the second egg in 256.1, and after the laying of each of the first three eggs in 251) (Fig. 1).

The establishment of continuous attentiveness also varied among nests. In three nests (256.2, 209 and 251) continuous attentiveness began during the night preceding the laying of the penultimate egg (Fig. 1). In 284 continuous attentiveness began during the day of the laying of the penultimate egg, while in 266 (with the 2-egg clutch), attentiveness began in mid-afternoon on the day of the laying of the last egg. In 256.1, the loss of data precluded identification of the beginning of continuous attentiveness, but it did begin before the laying of the last egg.

In conclusion, the results of this preliminary study clearly indicate that bouts of incubation begin during egg laying in the House Sparrow, usually with the laying of the first egg. These findings are consistent with the hypothesis that tactile feedback from the eggs (through the brood patch) may play a role in the mechanism controlling clutch size in the species (Anderson 1995). They also suggest that egg removal in experiments to test for determinate or indeterminate laying in a species should occur soon after egg laying to obviate the possible effects of tactile feedback from the egg on the termination of laying.

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TED R. ANDERSON, *Division of Science and Mathematics, McKendree College, Lebanon, Illinois 62254.* *Received 29 Feb 1996, accepted 14 Jan 1997.*

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Individual, brood, and sex variation in begging calls of Western Bluebirds.—Vocal differences in birds are often sufficient for recognition not only of species but of variables such as sex, age, genetic relatedness, and condition. Here we analyze begging calls of Western Bluebird (*Sialia mexicana*) nestlings and test for family, sex, and individual differences. The original impetus for this study was the finding by Gowaty and Droge (1990) that female Eastern Bluebird (*Sialia sialis*) nestlings were fed more often than were male nestlings and that female-biased broods were provisioned more frequently by the adult male attending the nest. If this result is due to an adjustment of parental behavior in response to the sex of the nestlings, then there must be a proximate mechanism by which parents can determine the sex of their offspring. Inasmuch as bluebirds are cavity nesters and nestlings are similar in size, the most likely mechanism for sex recognition is differences in nestling vocalizations or begging calls.

Subsequently, work in our study population has determined that sex-biased provisioning does not occur (Leonard et al. 1994) and, furthermore, that parents do not discriminate against unrelated offspring translocated into their nests (Leonard et al. 1995). These results prompt a somewhat different question than that originally envisioned. Given that Western Bluebird parents do not appear to discriminate among offspring, either on the basis of sex or genetic relatedness, are differences in nestling vocalizations uncorrelated with these factors? If vocalizations are not distinguishable between the sexes or between nests, then one

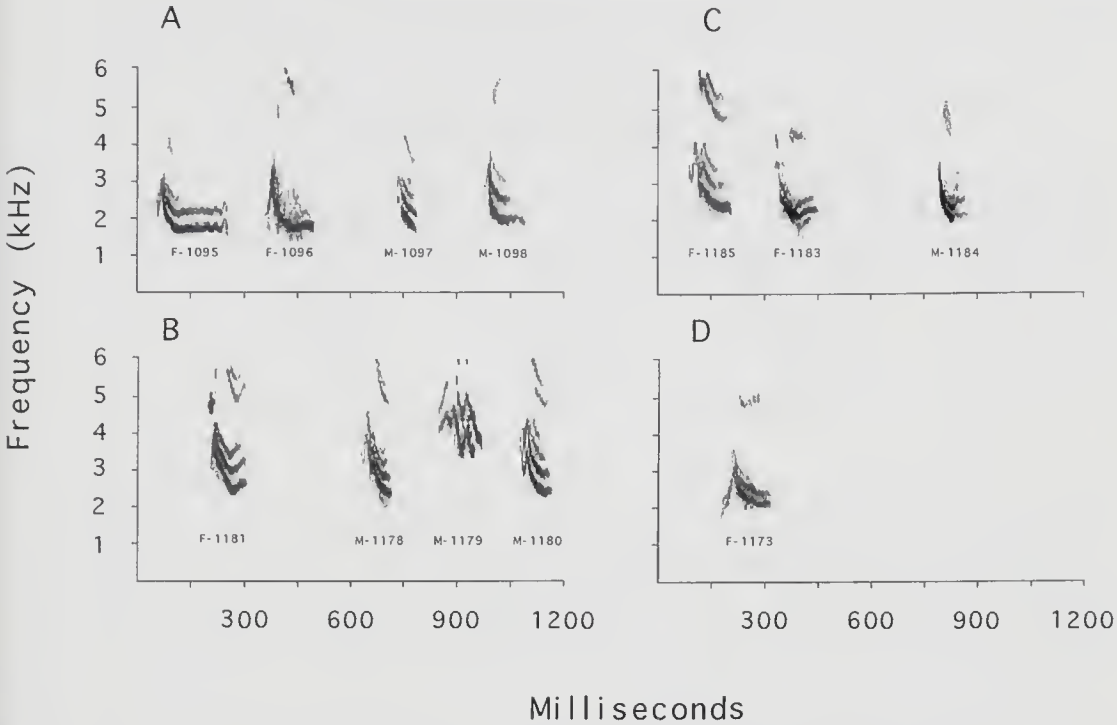

FIG. 1. Sound spectrograms of begging calls of 12 Western Bluebird nestlings from four different families (A, B, C, D). For each family, sound spectrograms on the left of the time scale represent calls of female nestlings (F-); sound spectrograms on the right of the scale represent calls of male nestlings (M-). Each sound spectrogram is a representative example for the begging calls of each nestling.

possible mechanism of discrimination would be absent in Western Bluebirds, even though such discrimination might be advantageous.

Methods.—We recorded nestling begging calls of Western Bluebirds at Hastings Natural History Reservation, Monterey Co., California, in June and July, 1989. All nestlings from three nests and one additional nestling from a fourth nest were recorded. Twelve nestlings were recorded in all, including six males and six females. Recordings were made when nestlings were between 14 and 19 days old, just after nestlings can be sexed by plumage (Pyle et al. 1987) and several days before fledging, which usually occurs when nestlings are about 21 days old.

We used an omnidirectional microphone (Sony ECM-280) mounted on the inside of the nest box and recorded several begging calls for each nestling before feeding by parents. The microphone was attached to a tape recorder operated from a blind 3–7 m behind the nest box. Nestlings were recorded individually by removing all chicks but the one that was being recorded; chicks not being recorded were held together in a bird-holding bag inside the blind. One chick after the other was placed into its nest box for recording. Chicks were kept in the nest box by themselves for no longer than 30 min., after which they were replaced with another chick from the brood. On two occasions we recorded two nestlings in the nest together to verify that chicks were giving the same calls when by themselves as when together.

Begging calls were analyzed using The Sound Analysis and Synthesis System on an AMIGA Micro-computer (Fig. 1). The calls were digitized using eight bits and a sampling frequency of 12 kHz (Richard 1991). Sound spectrograms were carried out by a fast Fourier transform using 256 points and weighted by a Hanning window (Richard 1991). Time and

TABLE 1

PROPORTION OF VARIATION AMONG INDIVIDUALS AND WITHIN INDIVIDUALS FOR PARAMETERS OF BEGGING CALLS OF WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	*F*-ratio (df = 11,113)	*P*	Percent variation between	Percent variation within
DOMF	152.7	<0.0001	93.6	6.4
DF	38.5	<0.0001	78.3	21.7
DT	15.5	<0.0001	58.3	41.7
F1	765.9	<0.0001	98.7	1.3

frequency were displayed at full (1×) scale, the tape recorder was set to full speed. All settings of the amplifier were at 0 dB, except 31 Hz and 16 kHz which were both set at −12 dB, in order to reduce background noise.

For all but two nestlings, we measured 11 different sonograms using calls that were maximally separated in time during the recording. In the remaining two cases we were able to obtain 10 and five calls, respectively.

We measured four parameters from each sonogram (comparable to Medvin et al. 1992, 1993): (1) the frequency at which the begging call is loudest (the dominant frequency, DOMF), (2) the duration of the begging call (DT), (3) the frequency range of the strongest band on the sonogram (DF), and (4) the lowest frequency of the strongest band on the sonogram (F1).

For each of the four vocalization parameters, we partitioned the variance within and among individuals with a one-way ANOVA in which "individual" was used as the main factor. Coefficients of intraclass correlations were calculated following Sokal and Rohlf (1981).

To test for a sex effect, we used a one-way ANOVA with "sex" as the main factor; means for each of the 12 nestlings were used rather than individual calls. The results of this analysis indicated no significant sex differences ($0.18 < P < 0.68$) (Table 2), and therefore we pooled across sex to the test for a nest effect. We tested for a nest effect using a one-way ANOVA with "nest" as the main factor.

Results.—Vocalization parameters were highly consistent within individuals, and most of the variation was found among individuals. For each of the four variables, a large (between 58.3 and 98.7%) and highly significant proportion of variance was attributable to individual differences (Table 1). Thus, nestlings had highly distinctive begging chirps.

Vocalization parameters exhibited no differences between the sexes (Tables 2, 3). In contrast, DOMF, the frequency at which begging was loudest, differed significantly among nests (Table 2). Variation among nests for F1, the lowest frequency of the strongest band, also approached significance.

Discussion.—These analyses indicate that begging calls of nestling Western Bluebirds differ significantly among individuals and among nests but not between male and female nestlings. Our failure to detect differences in the vocalizations of nestlings between the sexes is concordant with the results of Leonard et al. (1994), who found no evidence for biased provisioning with respect to sex of nestlings in the Hastings population.

Because we did not record begging calls of cross-fostered nestlings, we do not know the degree to which within-nest similarities in begging calls are determined by genetic similarity or by the common nest environment. If begging calls are primarily genetically determined, then parents could gain fitness advantages if they were able to recognize reliably and subsequently avoid wasting parental effort on unrelated nestlings (Owens 1993). Such unrelated

TABLE 2

RESULTS OF ANOVA TESTING FOR SEX AND NEST DIFFERENCES IN VOCALIZATIONS OF WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	Sex effect		Nest effect	
	F-ratio (df = 1,10)	*P*	*F*-ratio (df = 3,8)	*P*
DOMF	0.403	0.54	5.545	0.024
DF	0.187	0.675	0.546	0.665
DT	2.076	0.18	0.496	0.695
F1	0.823	0.386	3.241	0.082

nestlings do not arise via brood mixing in this cavity-nesting species, but rather from extra-pair fertilizations, which are relatively common in this population (J. L. Dickinson, unpubl. data). However, discrimination by bluebird parents between nestlings from their own nests versus nestlings translocated from other nests does not occur (Leonard et al. 1995). Thus, it is unlikely that adult bluebirds use brood-specific begging calls or individual differences in begging calls during the nestling stage to distinguish between related and unrelated young.

In contrast, mixing of family groups can occur following fledging while offspring are still dependent on their parents (D. Monk, unpubl. data). Thus, it is possible that parents use brood-specific and individual-specific begging calls at that stage to identify and discriminate against fledglings from other families mixed in with their own brood (Beecher 1990, Barg and Mumme 1994). Alternatively, brood-specific and individual-specific calls may confer no selective advantage when birds are young but may be used later in life for social interactions between mates and neighbors. Additional studies will be necessary to test possible fitness functions of brood-specific and individual-specific nestling calls as well as to understand the intriguing differences in parental behavior that have been reported for Western and Eastern bluebirds.

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TABLE 3

MEANS AND 95% CONFIDENCE INTERVALS (USING STUDENT'S *T*-TEST FOR SMALL SAMPLE SIZES) FOR VOCALIZATION PARAMETERS OF BEGGING CALLS OF FEMALE AND MALE WESTERN BLUEBIRD NESTLINGS

Vocalization parameter	Female nestings			Male nestlings		
	N	Mean	95% Confidence intervals	N	Mean	95% Confidence intervals
DOMF	6	2722	570	6	2994	873
DF	6	1802	336	6	1729	273
DT	6	137	27	6	120	18
F1	6	2155	378	6	2493	839

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DANIELA S. MONK, *Dept. of Biology and Program in Animal Behavior, Indiana Univ., Bloomington, Indiana 47405;* AND WALTER D. KOENIG, *Hastings Reservation, Univ. of California, 38601 E. Carmel Valley Rd., Carmel Valley, California 93924.* *Received 7 May 1996, accepted 12 Nov. 1996.*

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Communal roosting behavior of the Cave Swallow in El Salvador.—In autumn 1994, I located more than 5000 Cave Swallows (*Hirundo fulva*) at each of two nocturnal roost sites in El Salvador. Here I provide information on the communal roosting behavior of the species and roost-site characteristics on previously unknown wintering grounds in Central America. Roosting of many species of New World swallows has not been described. The winter roosting habits of migratory North American swallows likewise are sparsely known. This study provides the first description of the winter roosting habits of the Cave Swallow.

Study area and methods.—I conducted the study in a 2500 km^2 region of the coastal plain of El Salvador below 100 m elevation, from Río Paz, Ahuachapán, in the west (13°45′N, 90°08′W), to Estero El Espino, Usulután, in the east (13°10′N, 88°15′W). This area is mostly agricultural flatlands with little natural habitat, except for 38,000 ha of man-

grove forests associated with several large bays and estuaries. The coastal plain is interrupted by two small mountain ranges, the Cordillera del Bálsamo in the Department of La Libertad, and the Colinas de Jucuarán east of Estero El Espino. I did not survey the seacliffs or hills in these sections of the El Salvador coast. Climatic information for the study area is provided by Holdridge (1977), who placed it within the hot humid subtropical forest zone. This zone has a marked and regular rainy season from May to October. Rainfall during this period varies from 1400 mm to 2000 mm, or 270 mm average per month. In November, rainfall drops to 50 mm, and generally no accumulation is recorded for December through April. The median temperature from September through February is 26°C, with daily high temperatures often above 30°C.

I use the term "roost" to mean a "communal roost," a central sleeping area to which several dispersed groups or individuals converge, as defined by Ward and Zahavi (1973). I located roost sites by following swallow flocks in the late afternoon, and by triangulation when more than one flight line was evident. A team of four field assistants and I generally searched along the coast and coastal plain for foraging swallows 3–6 days a week between 4 Oct. and 10 Dec. 1994. We watched Cave Swallows flying to roost on eight evenings (four evenings at each of two sites). We located sleeping birds on two evenings at one site. I calculated the height of swallows circling above roost sites by estimating the angle at which I observed the birds at their zenith, and then measuring the distance between my observation point and their horizontal position (the roost site).

At one of the two swallow roost sites, I obtained six voucher specimens by searching for sick or dead birds at the roost site, and collecting sleeping birds by hand or with a hand-held dip net. The specimens are deposited at the Museo de Historia Natural de El Salvador and the Univ. of Kansas Natural History Museum. To determine the source population, I compared the six specimens to study skins from all known breeding populations of Cave Swallow.

Results.—I saw Cave Swallows on 14 out of 21 field days from 1 Nov. until the end of field work on 10 Dec. I saw none on nine field days preceding 1 Nov. I located one roost at the Hacienda Chahuantique south of Jiquilisco, Usulután (13°18′N, 88°35′W), and another at the Hacienda Monteshasta, 500 m north of Playa Miravalle, Sonsonate (13°37′N, 89°38′W). The roosts, each estimated by direct counts and extrapolation to hold 5000–8000 birds, were located 2.0 km and 0.6 km from the coast, respectively. At the first site, on 17 and 18 Nov., Cave Swallows dropped in to the roost over a cultivated field of sorghum (*Sorghum vulgare*, called maicillo by local farmers), but I could not see that they actually slept on the sorghum plants, which resemble corn. I saw about 140 Cave Swallows flying toward this roost on 1 Nov. at 17:05 h (CST), 5 km away at Puerto El Triunfo. At the second site, from 7–9 Dec., I observed Cave Swallows sleeping on the leaves of mature plants of a thin-stalked variety of sugar cane (*Saccharum officinarum*) known locally as "1312" in parts of a 28 ha cane plantation. I had seen more than 50 Cave Swallows flying toward this roost on 8 Nov. at 17:20 h, 2 km away near Barra Siega.

Cave Swallow behavior was similar on each of five evenings. Five to eight thousand Cave Swallows began appearing above the roost approximately 30 min before sundown and then seemed to forage in a loose flock covering as much as 1000 ha. They flew approximately 30 m above the ground, often chirping or emitting a song that resembled the warbling of captive Budgerigars (*Melopsittacus undulatus*). On the three evenings we were able to observe the flocks at close range (18 Nov., 8 and 9 Dec.), the swallows were quite vocal as they gathered above the roost, except when a Merlin (*Falco columbarius*) was nearby. No swallows of other species were detected at the roosts.

During the 30 min before sunset (approximately 17:30 h), the flock slowly became denser. At sunset the birds began to fly in one direction around the roost site, forming a large wheel.

The direction of revolution was not noted, but I recall it to be counterclockwise. The flock continued condensing, causing the wheel to shrink, at the same time gaining altitude with each revolution. After having risen about 1000 m in 15 min, the flock began to drop, rapidly spiraling downward, on several occasions forming a shape that looked like the funnel of a tornado. Groups would occasionally break the fall by swooping upward. During the descent, the swallows divided into groups of 50 to 200 birds which reached the roost at intervals between 17:48 and 18:10 h. The last birds to enter the roost circled more than 1000 m above the ground until about 40 min after sunset. As the groups reached about 5 m above the ground, having dropped at a very steep angle, their path of descent leveled off with the birds planing nearly horizontally over the roost and dispersing in several directions. It was virtually dark when most birds entered, and many groups arrived unobserved. At both roosts I conservatively estimated that the swallows attained a height of 1000 m prior to settling, but some may have reached as much as 1500 m. While I observed the roost from a distance of between 1000 and 1500 m, the birds reached about 45° above the horizon.

Groups of swallows settling at different times occupied separate "patches," or sections, of the cane field, often separated from other groups of roosting swallows. At the Playa Miravalle roost, these patches were spread over an area of at least 14 ha (350 m × 400 m) of cane field. Of 25 Cave Swallows I observed perched in the sugar cane roost, only four (two groups of two) were close to other birds (minimum distance 30 cm). The birds perched an average 2.5 m above the ground (N = 10, SE = 0.1 m, range 2.0–3.0 m) on both green and dead leaves. The height of the cane plants ranged from 3.0 m to 4.5 m.

The history of the cane field suggests that the roost site changes frequently. The cane was planted only 12 months earlier. Part of the roosting area was scheduled for burning and harvesting beginning on 12 Dec. The roost therefore had to move, but cane fields in this region mature at various times between November and March, and adjacent lots suitable for swallow roosting would be available during this time period. If roosting takes place in sorghum, swallows would also encounter harvesting in December and possibly January. Sorghum fields are rotated to other crops, so the swallows would have to seek another roost substrate such as sugar cane.

I observed two instances of mortality. One Cave Swallow killed by a dog on or near the beach on 8 Dec. was probably ill or severely fatigued. It weighed only 14.5 g, 25% less than the five other specimens examined. The bird may have just completed its migration, arriving exhausted. Only once did I see Cave Swallows on the ground, at the impoundments of the El Zope experimental mariculture station, where a flock of swallows had briefly landed in a dry, salty impoundment, fluttering their wings above them in a posture typical of mud-gathering. A second mortality at the roost site occurred when a Cave Swallow collided with nearby electrical lines on 9 Dec.

Discussion.—Of the North American swallows, the Barn Swallow (*Hirundo rustica*), Tree Swallow (*Tachycineta bicolor*), and Purple Martin (*Progne subis*) are known to sleep in large communal roosts on the wintering grounds (Forbush 1929, Rudebeck 1955, Haverschmidt 1968, Hill 1988, Ridgely and Tudor 1989, Hill 1993). Neotropical species often sleep in small family-sized groups (Skutch 1989), although large communal roosts have been reported for four species: Gray-breasted Martin (*Progne chalybea*) (Cherrie 1916, Dickey and van Rossem 1938, Hill 1988, pers. observ.), Southern Rough-winged Swallow (*Stelgidopteryx ruficollis*) (Skutch 1989), White-winged Swallow (*Tachycineta albiventer*) (Cherrie 1916), and Black-collared Swallow (*Atticora melanoleuca*) (Cherrie 1916).

All six El Salvador specimens of Cave Swallow belonged to the race *H. f. pelodoma*, which breeds in Texas, New Mexico, and northeast México. Cave Swallows roost at breeding caves during and shortly after nesting in Texas (Selander and Baker 1957) and New Mexico (West 1995). Cave Swallows from this or any other population have never been reported

roosting in vegetation. In one respect, the roosting behavior of the Cave Swallows differed markedly from other swallow species. Under natural conditions, communally-roosting swallows have been reported sleeping in close proximity to others of their own species, sometimes in physical contact (Bates 1895, Sage 1895, Weir and Weseloh 1986, pers. observ. of Gray-breasted Martins). In contrast, the Cave Swallows observed in this study slept widely dispersed, with each bird usually occupying its own space of many square meters. I have not encountered a description of individual swallows sleeping widely dispersed within a roost as in the Cave Swallow roost at Miravalle. While we could discern no direct effect of a falcon that was present on this "individual" distance, a case has been reported where Barn Swallows, roosting as one flock in a corn field, split into several roosting groups when a predator (also a falcon) was present (Rolls and Rolls 1977).

Other aspects of the roosting behavior of the Cave Swallows were similar to behavior described for several other swallows. For example, I observed in the Cave Swallows the same three phases described by Loske (1984) for Barn Swallow pre-settling flight behavior: initial aimless flight by many individuals, formation of a tight flock with subsequent acrobatic maneuvers, and the final descent. Barn Swallows and Southern Rough-winged Swallows also form communal roosts in sugar cane (Haverschmidt 1968, Ridgely and Tudor 1989, Skutch 1989). Similarly, these two species also perform elaborate group flight patterns, attaining great height before spiraling down into their roosts after sunset (Bent 1942, Skutch 1989). Just as I have described Cave Swallows singing in flight as they gather over the winter roost site, Selander and Baker (1957) described them singing in flight above cave entrances during the breeding season in Texas. They described a "complex melodic warble" lasting three seconds. I never heard Cave Swallow vocalizations while they foraged away from roost sites. After alighting in the roost, the swallows were silent. In contrast, Barn Swallows have been described as most vocal *after* settling in nighttime roosts (Bates 1895; Bent 1942; Loske 1984, 1986). Purple Martins also vocalize after gathering in the roost (Fisher 1907, Forbush 1929, Stone 1937).

Cave Swallow roosting behavior seems specialized for avoiding discovery: although they are noisy and evident at sunset, they disappear from the roost by flying up and out of range of unaided human vision before returning to sleep. They silently enter the roost after dark and sleep dispersed over a large area in a virtually unpenetrable habitat. We located only 25 perched Cave Swallows in 4 h of nighttime searching along the edges of the cane fields. The twisting, high-speed aerial dive performed just before entering the roost may serve to discourage predation, as was suggested for starlings and other communally-roosting species by Zahavi (1971).

The information-centre theory of Ward and Zahavi (1973) has been shown to explain communal breeding and foraging behavior in the Cave Swallow's close relative, the Cliff Swallow, *H. pyrrhonota* (Brown 1988). The theory also appears to fit the observed roosting behavior of the Cave Swallow and would suggest the presence of additional roost sites. By regularly switching among established roosts, individual birds learn more about potential feeding sites. The theory holds that the commune thus advertises itself to attract daily newcomers, who contribute new knowledge of food resources to the entire commune. Roost advertising was evident in the pre-settling flight behavior of Cave Swallows, as the birds were noisy and visible from a relatively great distance (Ward and Zahavi 1973). The two roosts discovered so far are separated by about 150 km and a small mountain range and are thus unlikely to provide regular interchange of commune members. I suspect several additional roosts existed within the study area.

Weatherhead (1983) disputed the qualification of complex flight displays as roost advertising behavior and suggested instead that the pre-settling flight displays of communally-roosting birds is a "jockeying for position and testing of status" to establish a dominance

hierarchy. But in the Cave Swallow, and perhaps other communally-roosting swallows, I suggest that both Ward and Zahavi's and Weatherhead's theories apply. Weatherhead's hypothesis applies best to the downward spiralling, when darkness and altitude must reduce the "advertising" effect of the flight behavior, and the impressive group flight acrobatics seem appropriate for a competition of dominance.

This study provided the first description of winter roosting behavior of the Cave Swallow and demonstrated that the winter distribution of the Texas and northeastern México race *H. f. pelodoma* includes the Pacific coastal plain of El Salvador. It remains to be determined, however, the full size of the winter population of the Cave Swallow in El Salvador, including specific locations of additional roost sites.

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OLIVER KOMAR, *Dept. of Zoology, Ohio Wesleyan Univ., Delaware, Ohio 43015.* *Received 20 March 1996, accepted 21 Sept. 1996.*

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Piping Plovers produce two broods.—Piping Plovers (*Charadrius melodus*) typically raise only one brood per season, although they may renest if the first clutch is destroyed (Wilcox 1959, Cairns 1982, Haig 1982). Other Charadriidae such as Killdeer (*Charadrius vociferus*) and Snowy Plover (*Charadrius alexandrinus*) are known to raise two broods per season if early nest attempts are successful (Nickell 1943, Warriner et al. 1986). The following observations may be the first documentation of Piping Plovers successfully producing two broods in a single breeding season.

Piping Plovers were observed at two sites. Griswold Point, owned and managed by the Nature Conservancy, is a 1.5 km × 30 m-wide barrier beach on Long Island Sound at the mouth of the Connecticut River in Old Lyme, Connecticut (utms 73000 m N, 24000 m E). Nesting activity has been consistently located on a 30 m × 300 m section of the beach. The second site, Assateague Island National Seashore (NS), is on barrier island situated along the coast of Maryland and Virginia. The 35 km Maryland portion of Assateague Island is primarily owned by the National Park Service (NPS), with additional ownership by the Maryland state park system (utms 424500 m N, 49500 m E). The northern section (9.5 km × 550 m on average) of Assateague Island is managed by the NPS as a primitive area with limited access and is the primary Piping Plover nesting area.

Griswold Point has been intensively monitored since 1982, with an average of three pairs of plovers nesting annually. The area was almost devoid of vegetation and could easily be surveyed. Observers distinguished individual birds by distinctive color patterns, particularly neck bands, and the birds' use of particular territories. Before 1991, some Piping Plovers were observed with a single United States Fish and Wildlife (USFWS) metal leg band. Piping Plover monitoring was initiated at Assateague Island National Seashore in 1985, with an average of 21 breeding pairs annually. In 1994, at Assateague Island National Seashore,

seven plovers had either an USFWS metal leg band or an individual combination of color leg bands, which allowed for their definitive identification.

Observations.—In 1989, one of three pairs of Piping Plovers at Griswold Point was observed with a nest that hatched four eggs on 14 May and fledged two young on 14 June. Between 1 and 17 June, this pair was observed engaged in various nesting behaviors (e.g., false incubation, making scrapes). On 19 June, the same pair (the other two pairs were observed actively incubating) laid another clutch with four eggs, three of which hatched on 12 July and fledged 8 August. On 20 and 23 June, the male from the second nest was observed with the fledglings from the first nest, supporting the theory that the same adults were involved.

In 1990, four breeding birds had USFWS metal leg bands, which were not read, but helped distinguish them from other Piping Plover at Griswold Point. One of the two breeding pairs of plovers at Griswold Point hatched young 24 May and fledged three birds. This first pair of Piping Plover moved their young more than 300 m into the second pair's territory (the second pair was observed brooding three hatchlings) on 16 June. From that date through 24 June, the first pair was observed courting, making scrapes, defending a territory, and mating. The first pair laid a second clutch 27 June and hatched three young 22 July, of which one fledged.

In 1991, one of three successful breeding pairs of Piping Plovers at Griswold Point hatched four young 27 May and began another clutch on 26 June with only one egg which failed. In 1992, one of five nesting plover pairs at Griswold Point was observed 1 May on a nest with four eggs which hatched 24 May and all successfully fledged. This pair laid another clutch 26 June and hatched three chicks 19 July but were not observed thereafter. A second pair laid four eggs by 6 May, which hatched 29 May and all successfully fledged. This second pair then laid four eggs, one of which hatched 29 May and all successfully fledged. This second pair then laid four eggs, one of which hatched 22 July and fledged.

In 1994, a pair of Piping Plovers at Griswold Point was observed with a nest 14 May. From this complete clutch, three eggs hatched on 24 May and two chicks fledged on 21 June. On 14 June this breeding pair was observed, in the presence of the chicks, exhibiting courtship postures (Cairns 1982) and mating. This pair subsequently nested 75 m from its original nest site. On several occasions, chicks from the first brood were observed with one adult within 1 m of the other adult incubating the active nest. On 21 June, the chicks from the first brood and the breeding pair were all observed within the predator exclosure erected around the active nest. Eggs from the second clutch hatched on 16 July and all later fledged. Although some efforts in 1991 and 1992 did not indicate a successful second attempt, it shows consistency in the effort. The remaining observations on banded and unbanded birds strongly indicate that some Piping Plovers at Griswold Point have been successful in raising two broods in a given season.

In 1994, at Assateague Island National Seashore, a female Piping Plover with three color leg bands and an USFWS metal leg band completed a four egg clutch on 15 April. Two eggs hatched on 22 May, and those chicks fledged on 16 June. On 30 July, the same banded female was observed incubating a second nest with three eggs located 10 m from the first nest. On 3 August, three chicks hatched and later fledged. The adult male of both these nests was unbanded, therefore absolute determination of the male's identification was impossible. There were several factors that indicated that the male was the same mate; the two nests were less than 25 m apart, there was not another pair or single male ever observed courting in this area (the nearest territory was 250 m away), and the neckband of the two mates appeared to be the same.

In a second situation at Assateague Island National Seashore in 1994, two color-banded birds nested 22 April, and four eggs hatched 25 May, of which one chick fledged. This

same pair was observed copulating 14 June with their unfledged chick present. On 10 August, the male was observed in his same territory engaged in distraction behavior, typical of adults protecting chicks, when two chicks (~20 days old) emerged from the surrounding vegetation. No adult female was present. All other known broods were accounted for, indicating that this was a newly discovered brood. This male and the two chicks (newly fledged) were observed 16 August 1 km away from the last sighting. These observations compelled the technicians to believe that this bird helped produce two successful broods.

Observations at both sites indicate that Piping Plover can successfully raise two broods in a single breeding season. This may have been facilitated by predator exclosures around nests or a decrease in predators in the nesting areas. In past years, heavy nest predation at these locations could have been potentially limited the success of a second brood. It is also possible that the adults that produced and reared double broods were more experienced and physically mature (banded birds were at least four years old) than most of the existing population. In addition, increased availability and/or access to feeding areas may have contributed to reproductive success.

The authors believe it will be difficult to ascertain the extent of double brooding in Piping Plovers. Banding of Piping Plovers ceased in 1989 and therefore the number of living banded Piping Plover is decreasing annually which will make it more difficult to determine individual birds. The ability to raise successfully two broods may be a factor in the management and recovery of this species which is currently listed by the USFWS under the Endangered Species Act.

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GRACE E. BOTTITTA, *Assateague Island National Seashore, 7206 National Seashore Lane, Berlin, Maryland 21811* (present address: *P.O. 312, Homer, Alaska 99603-0312);* ANDREW M. COLE AND BETH LAPIN, *The Nature Conservancy, 55 High Street, Middletown, Connecticut 06457* (present address AMC: *Yale University School of Forestry and Environmental Studies, Sage Hall, 205 Prospect Street, New Haven, Connecticut 06511).* *Received 12 June 1996, accepted 10 Oct. 1996.*

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Response of six species of Hawaiian forest birds to a 1991–1992 El Nino drought.—El Nino-Southern Oscillation events (ENSO) are known to effect reproduction and survival

of various bird species and other animals (Barber and Chavez 1983, Grant and Grant 1987, Hall et al. 1988, Massey et al. 1992). Although severe storms resulting from ENSO can directly cause bird mortality, primary effects appear to be influences of weather on food resources. During ENSO, precipitation is enhanced in some regions and diminished in others (Philander 1992). Enhanced rainfall may cause abundant seed crops and high arthropod populations, resulting in prolonged breeding seasons for some bird species (Gibbs and Grant 1987) or, along with reduced temperatures, decreases invertebrate populations resulting in breeding failure and reduced adult survival in other bird species (Miskelly 1990).

In Hawaii, ENSO generally causes rainfall to diminish (Philander 1992). Between 1941 and 1983, Hawaii has experienced six major ENSO droughts (Chu 1989). However, despite the periodic occurrence of ENSO droughts, few data are available about the effects on Hawaiian bird species. Here, we report a short-term effect of the 1991–1992 ENSO drought on capture rates, fat scores, and active nests of six resident Hawaiian forest bird species.

Study area and methods.—We conducted this study on the Island of Hawaii in the dryland mamane (*Sophora chrysophylla*)-naio (*Myoporum sandwicense*) forest near Puu Laau (19°50′N, 155°35′W) on the southwestern slope of Mauna Kea. Vegetation in the study area was described by van Riper (1980a) and Scowcroft and Giffin (1983). In 1991–1992, an ENSO throughout the Hawaiian Islands chain resulted in a nine-month drought from October through June. Total rainfall (<67 mm) in our study area was approximately 17% of average (Juvik et al. 1993; NBS, unpubl. data). The result of this drought was a general failure of flower and mamane seed set in our study area during 1992 (NBS, unpubl. data). Green seeds from mamane pods are a major food source for the endangered Palila (*Loxioides bailleui*); birds also use the nectar and flowers of mamane for food.

From April through September 1991–1993, we operated 10 mist nets at each of four fixed banding stations to capture birds within the study area. Nets were opened 1–4 days monthly at each banding station. Each bird captured was identified to species, marked with a USFWS aluminum band, and scored for visible fat within the furcular region before being released. Fat scores ranged from zero for no visible fat to four for the interclavicular fossa bulging with fat. We searched for active nests by walking 24 strip transects (each 40 m × 1 km) at monthly intervals during the same six-month period each year. A nest was considered active if eggs or nestlings were found. Capture data were compared by the paired comparison *t*-test and fat scores by the Mann-Whitney *U* test (Sprent 1993).

Results.—The overall capture rate (number of birds per 100 net-h) for the six species combined was 49.9 for 1991 (N = 2913 net-h), 19.2 for 1992 (N = 4361 net-h), and 47.5 for 1993 (N = 3439 net-h). During 1992, the overall capture rate was 60% lower than in 1993 and 62% lower than in 1991. Mean monthly capture rates for 1992 were lower ($P < 0.05$) than those for 1991 for Hawaii Amakihi (*Hemignathus virens*), Palila, Japanese White-eye (*Zosterops japonicus*), and House Finch (*Carpodacus mexicanus*) (Table 1). Mean monthly capture rates for 1993 increased ($P < 0.05$) compared to 1992 for Hawaii Amakihi and House Finch. Capture rates for 1993 for Japanese White-eyes did not return to pred-rought levels, but remained lower ($P < 0.05$) compared to 1991.

Fat scores in 1992 were less ($P < 0.05$) for Hawaii Amakihi, Palila, Elepaio (*Chasiempis sandwichensis*), and Japanese White-eyes when compared with fat scores from 1991 (Table 2). For Red-billed Leiothrix (*Leiothrix lutea*), fat scores in 1992 were similar to those of 1991 and larger ($P < 0.05$) than those in 1993.

During 1992, Hawaii Amakihi and Palila nesting attempts decreased 96% and 93%, respectively, compared with 1991 data (Table 3). Sample sizes for the remaining four species were low, but data suggests that nesting attempts for the Red-billed Leiothrix and House Finch may also have been reduced.

Discussion.—Environmental perturbations caused by ENSO have significant short- and

TABLE 1

MEAN MONTHLY CAPTURE RATES (NUMBER BIRDS PER 100 NET-H) FOR SIX RESIDENT BIRD SPECIES ON MAUNA KEA, HAWAII, APRIL–SEPTEMBER, 1991–1993[a]

Species	Year		
	1991	1992	1993
Hawaii Amakihi[b]	38.7a	15.5	44.8a
Palila[b]	2.3a	0.9b	1.9ab
Elepaio[b]	1.3a	0.4a	0.5a
Japanese White-eye[c]	3.4	0.9a	1.0a
Red-billed Leiothrix[c]	2.4a	1.0a	0.9a
House Finch[c]	1.2a	0.1	0.7a

[a] Between October 1991 and June 1992, the study area experienced a nine-month ENSO drought. Means with the same letter are not significantly different (paired comparison *t*-test, $P < 0.05$).
[b] Native Hawaiian species.
[c] Alien species.

long-term effects on the demography of both marine and terrestrial bird species (Barber and Chavez 1983, Schreiber and Schreiber 1984, Hall et al. 1988). Field biologists studying terrestrial species must be aware that ENSO may effect study regions and species far removed from marine ecosystems (Schreiber and Schreiber 1984) and could be an important selective determinant of life-history traits (Hall et al. 1988).

During an El Nino drought in Panama in 1983, Karr et al. (1990) reported that bird capture rates in his study area were the most extreme ever recorded during eight years of sampling. In two relatively dry study plots, capture rates were the lowest recorded, while one wetter study plot had the highest capture rate recorded for a dry season sample. In our study area, the 1991–1992 ENSO drought reduced capture rates for four species, reduced fat levels for four species, and reduced nesting attempts for at least two species. The primary

TABLE 2

MEAN MONTHLY FAT SCORES FOR SIX RESIDENT BIRD SPECIES ON MAUNA KEA, HAWAII, APRIL–SEPTEMBER, 1991–1993[a]

Species	Year					
	1991		1992		1993	
	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)
Hawaii Amakihi	673	2.25 (0.78)	568	1.93 (0.99)	960	2.19 (0.96)
Palila[b]	64	2.23 (0.77)	33	1.97 (0.88)	61	2.43 (0.83)
Elepaio[b]	21	1.62 (0.80)	18	1.00 (0.84)	17	1.65 (1.00)
Japanese White-eye[c]	49	2.20 (0.73)	26	1.61 (1.13)	27	2.11 (0.80)
Red-billed Leiothrix[c]	36	1.58 (0.98)a	30	1.60 (1.10)a	25	1.12 (1.36)
House Finch[c]	16	1.81 (0.98)	5	2.40 (0.55)	19	1.58 (1.43)

[a] Between October 1991 and June 1992, the study area experienced a nine-month ENSO drought. Means with the same letter not significantly different (Mann-Whitney *U*-test, $P < 0.05$).
[b] Native Hawaiian species.
[c] Alien species.

TABLE 3

NUMBER OF ACTIVE NESTS FOR SIX RESIDENT BIRD SPECIES FOUND IN 24 TRANSECTS (EACH 40 M × 1 KM) ON MAUNA KEA, HAWAII, APRIL–SEPTEMBER 1991–1993[a]

Species	Year		
	1991	1992	1993
Hawaii Amakihi[b]	163	6	27
Palila[b]	71	5	70
Elepaio[b]	1	0	0
Japanese White-eye[c]	1	1	4
Red-billed Leiothrix[c]	12	5	4
House Finch[c]	12	4	8

[a] Between October 1991 and June 1992, the study area experienced a 9-month ENSO drought.
[b] Native Hawaiian species.
[c] Alien species.

effect of this ENSO drought on resident birds in our dryland forest was presumably caused indirectly through food resources being reduced. From other studies, the number of nesting attempts by Palila is known to be influcnced by annual differences in precipitation and availability of immature mamane pods (Van Riper 1980b; NBS, unpubl. data). Adult Palila had lower survival in years when mamane seed production was low (Lindsey et al. 1995).

On Mauna Kea, the Hawaii Amakihi population is intrinsically tied to its food supply, particularly nectar resources (van Riper 1984, 1987). Hawaii Amakihi has a protracted nesting season from November to July, but initiation of the breeding season is variable and coincides with major mamane flowering periods. Between breeding periods, most Hawaii Amakihi pairs undergo postbreeding dispersal which corresponds to the cessation of mamane flowering. Our data indicated fewer active nests for Hawaii Amakihi in 1993 than in 1991. However, Hawaii Amakihi nesting peaked in the winter and early spring following the El Nino drought, as indicated by the large number of juvenile birds captured and vacant nests found in the spring and summer of 1993 (NBS, unpubl. data). This peak in nesting coinciding with the peak mamane flowering period for that period.

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GERALD D. LINDSEY, THANE K. PRATT, MICHELLE H. REYNOLDS, AND JAMES D. JACOBI, *United States Geological Survey, Biological Resources Division, Pacific Islands Ecosystems Research Center, Hawaii Field Station, P. O. Box 44, Hawaii National Park, Hawaii 96718.*
Received 15 Aug. 1996, accepted 10 Oct. 1996.

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Daily variation in activity and flock size of two parakeet species from southeastern Brazil.—Psittacids are wide-ranging birds usually occurring in large flocks, making direct density estimates of parrots difficult. Researchers often are obliged to rely on indirect methods to estimate their abundances (see Terborgh et al. 1990, Pizo et al. 1995). These estimates are based on the number of flocks contacted in a given period (average encounter rate) and on the mean flock size of the species considered. However, both measures can vary on a daily basis (Blake 1992, Cannon 1984, Chapman et al. 1989), implying that parrot counts should be concentrated in a given period of the day to save time and to ensure a more realistic estimate (Blake 1992). Some attempts have been made to assess daily variation in detectability of Neotropical parrot species (Blake 1992). This author noted that detections of canopy bird species, such as parrots, tend to increase from the first to second hours after sunrise in a tropical wet forest in Costa Rica. Hourly variation in flock sizes of parrots, however, has hitherto received little attention. Chapman et al. (1989) observed that mixed-species flocks of parrots in Costa Rica were significantly larger during late afternoon, just before they move to a communal roosting site, than at other times of the day.

Here we report on the daily activity and flock size of two common parakeet species occurring in the Atlantic forest of southeastern Brazil, the Maroon-bellied Parakeet (*Pyrrhura frontalis*) and the Plain Parakeet (*Brotogeris tirica*). We address the following ques-

tions: (1) Do flock sizes vary on a daily basis? and (2) Does such variation differ among seasons?

Maroon-bellied Parakeets (26 cm length, 85 g weight) and Plain Parakeets (23 cm length, 80 g) are the most abundant parrots at our study site (Pizo et al. 1995) and are among the most common ones in southeastern Brazil, where the latter species can occur even in urban areas (Ridgely 1981; pers. obs.). Flock sizes of Maroon-bellied Parakeet at the study site range from 1 to 34 ($\bar{x}$ = 5.1 ± 3.8 SD, N = 499) and those of Plain Parakeet from 1 to 40 ($\bar{x}$ = 4.5 ± 4.2 SD, N = 438) (Pizo et al. 1995). These flocks are regularly seen flying over the canopy. Populations of both species decline during the dry seasons, probably due to habitat shifts (Pizo et al. 1995).

Study site and methods.—We carried out this study at Parque Estadual Intervales (PEI hereafter), Ribeirão Grande, São Paulo State (24°16′S, 48°25′W), a 49,000 ha reserve in the Serra de Paranapiacaba mountains of southeastern Brazil at an elevation of 700 m. The vegetation there was composed of primary forest with 30 m trees and patches of second growth near human settlements. The climate generally is wet, with rain or fog ocurring frequently. Annual precipitation is around 1600 mm with a dry season from April to August (winter), when the temperature often drops below 5°C and frosts may occur, and a wet season from September to March. Seasonal variation in temperature is pronounced, ranging from a minimum mean temperature of 13.4°C in winter to 21.6°C in summer. Sunrise occurred between 05:11 and 06:18 h in the wet seasons and between 06:15 and 06:45 h in the dry seasons.

We counted flocks from Dec. 1989 to Dec. 1991, and from August 1992 to January 1994 during monthly visits (4–10 days each) to PEI. We looked for the parakeets during walks conducted along several trails (approximately 20 km) that cross the study site. These walks were distributed between 06:00 and 18:00 h, and usually lasted for 4–5 h. Overall, about 533 and 366 h were spent conducting counts in wet and dry seasons, respectively. Whenever a flock was encountered we recorded the species, flock size, and time of day. The hourly mean flock size was based only on flocks which were seen and which could be counted. As parakeet populations declined during the dry seasons, we recorded few flocks per hour. Consequently, inter-seasonal comparisons of mean flock size were based on flocks observed during three four-hour categories: morning (06:00–09:59 h), midday (10:00–13:59 h), and afternoon (14:00–17:59 h) flocks.

We used the hourly average encounter rate (AER) as a measure of activity. AER was based on data collected from August 1990 to December 1991, encompassing two dry and two wet seasons (289 and 198 h of field time in the wet and dry seasons, respectively). AER was based on aural and visual detections, i.e., on all flying or perched flocks seen or heard during walks.

We used parametric one-way ANOVA followed by a Tukey multiple comparison test to detect hourly differences in mean flock sizes. A t-test was used for inter-seasonal comparisons of mean flock size. Data on flock size were log-transformed to achieve normality prior to statistical tests. All tests follow Zar (1984).

Results.—During the study of daily AER, we detected 708 and 961 flocks of Maroon-bellied and Plain parakeets, respectively. AER of both species varied during the day, particularly during the wet season (Fig. 1A and B). Maroon-bellied Parakeets were detected more frequently in the second and third hour after sunrise during the wet season, and experienced a decrease in detectability of 23–47% between 09:00 and 11:00 h. A second peak in activity was recorded just after 12:00 h. In the dry season, AER varied less during the day with a slight decrease around 12:00 h (Fig. 1A). In contrast, Plain Parakeets were detected most often just after dawn during the wet season, experiencing a 40% decrease in

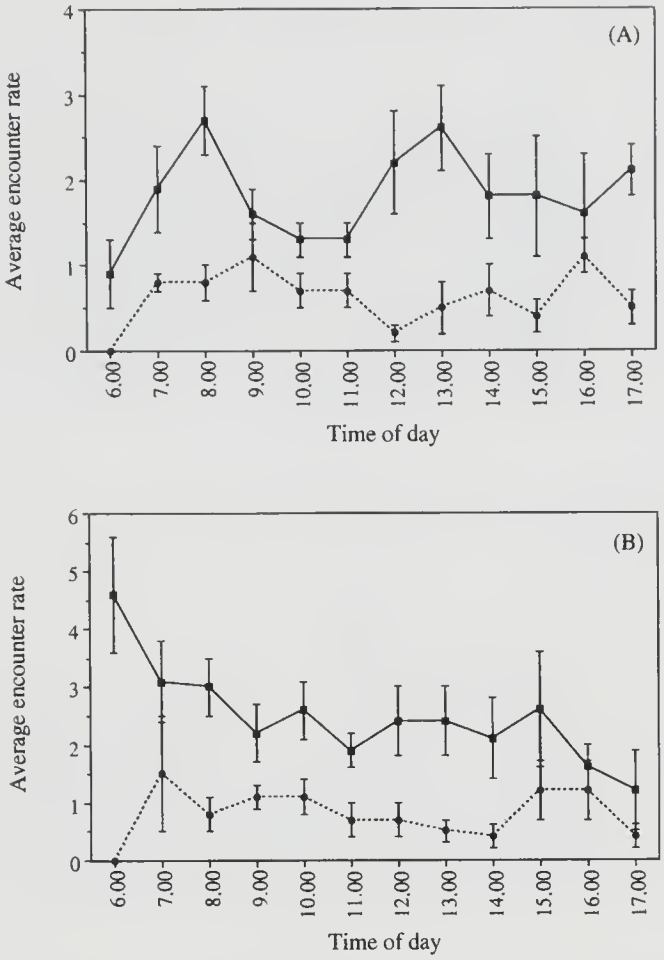

FIG. 1. Daily variation in the average encounter rate of (A) Maroon-bellied Parakeet and (b) Plain Parakeet during the wet (solid line) and dry (dotted line) seasons at Parque Estadual Intervales. Vertical lines represent standard errors.

detectability one hour later. In the dry season, Plain Parakeets were also uniformly detected through the day (Fig. 1B).

Combining data from wet and dry seasons, mean flock size of Maroon-bellied Parakeets did not differ during the day ($F = 0.91$, $df = 11$, $P > 0.50$) (Fig. 2A), but mean flock size of Plain Parakeets did ($F = 1.92$, $df = 11$, $P < 0.05$) (Fig. 2B). A Tukey multiple comparison test showed that the mean flock size of Plain Parakeet was significantly lower from 10:00 to 12:00 h, when 82% of the counted flocks ($N = 11$) were composed by one or two birds, than during other hours.

Considering morning, mid-day and afternoon periods, there were no inter-seasonal differences in mean flock size of either species except for afternoon flocks of Plain Parakeets (Table 1). Plain Parakeet flocks observed between 14:00 and 17:59 h were smaller during the dry than during the wet season.

Discussion.—Daily activity patterns of birds in general are influenced by several factors, including weather, season, and habitat (see references in Ralph and Scott 1981) but patterns are likely to differ among species (Blake 1992, Blake et al. 1991, Cannon 1984, Robbins 1981). Our data indicate that daily activity (here considered in terms of vocal, flying, and

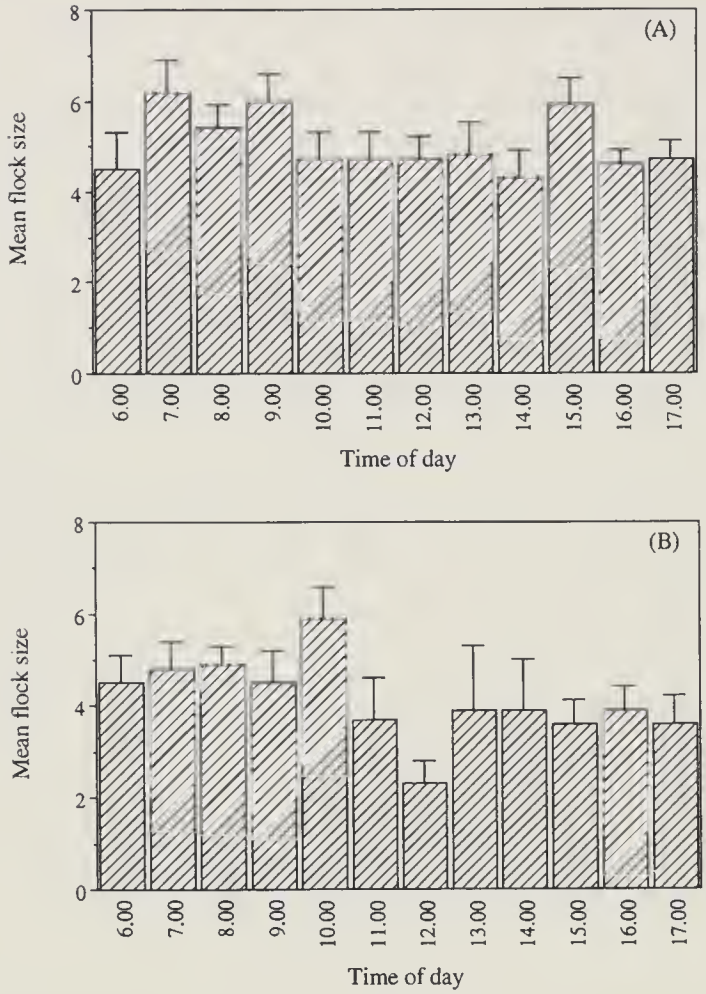

FIG. 2. Daily variation in mean flock size of (A) Maroon-bellied Parakeet and (B) Plain Parakeet at Parque Estadual Intervales. Standard errors are shown.

TABLE 1

MEAN SIZE (±SD) OF FLOCKS OF MAROON-BELLIED AND PLAIN PARAKEETS DURING THE WET AND DRY SEASONS AT PARQUE ESTADUAL INTERVALES

	Maroon-bellied Parakeet		Plain Parakeet	
Period	Dry season	Wet season	Dry season	Wet season
Morning	6.4 ± 4.6 (43)	5.5 ± 4.6 (145)	4.0 ± 2.6 (22)	4.8 ± 4.4 (230)
Mid-day	5.4 ± 3.7 (23)	4.5 ± 3.2 (106)	3.1 ± 2.8 (13)	4.9 ± 4.7 (72)
Afternoon	5.6 ± 2.7 (43)	4.7 ± 3.4 (121)	2.1 ± 0.7 (20)***	4.0 ± 3.4 (93)

*** *t*-test applied to log-transformed data: $P < 0.001$; Sample sizes are in parentheses.

foraging activity) and flock size of two parakeet species vary both hourly and seasonally. In addition, daily activity differed between both species, particularly during the wet season.

Roth (1984) suggested that the daily activity of parrots may be influenced by temperature, particularly in summer. This author observed a decrease in flying and feeding activity of 16 parrot species during the hotter hours of the day (11:00–14:00 h) in an Amazonian forest site. In fact, many parrot species exhibit a period of general inactivity during the hotter hours of the day (Hardy 1965, Snyder et al. 1987 and references there in) when they typically spend their time resting amidst the vegetation, where they are difficult to locate (Snyder et al. 1987). During the present study, Maroon-bellied Parakeets were very active, flying and vocalizing, during the second and third hours after sunrise during the wet season, but decreased their activity coincidently with the beginning of the hotter period of the day (09:00–15:00 h). However, their activity level increased again while the air temperature was still very high (just after midday). Plain Parakeets, on the other hand, were most active during the first hour after sunrise, but did not become active again even when the air temperature decreased during late afternoon (17:00–18:00 h). The hotter conditions that typically prevail during the wet season undoubtedly contributed to the well-marked daily activity patterns then observed. The low temperatures occurring in the dry season (winter) may have accounted for the more uniform daily activity patterns during that season. However, such a relative uniformity should be interpreted with care because the low abundance of parakeets during the dry seasons (Pizo et al. 1995) might have masked daily activity patterns.

The hourly variation in mean flock size of Plain Parakeets is somewhat intriguing. It is also possible that the high temperatures registered between 10:00 and 12:00 h play a role on the small flocks recorded during this period.

The smaller afternoon flocks of Plain Parakeets during the dry seasons may be related to the previously cited lower overall population densities of this species during the period (Pizo et al. 1995). However, factors other than population densities or weather conditions also may influence daily variation in flock size. During the breeding period, for example, flocks tend to be smaller than at other times because breeding pairs often keep separate from other individuals (Cannon 1984, Chapman et al. 1989, Rodriguez-Estrella et al. 1992). At our study site, reproduction takes place in the wet season (Forshaw 1989), but we failed to detect any effect on flock size associated with breeding. It is possible that breeding pairs of the species studied here travel with flocks more often than do larger parrots such as members of *Amazona* genus (see Martuscelli 1995, Snyder et al. 1987).

Future studies that address the distribution patterns of daily flock sizes of parrots should take into account the environmental (e.g., temperature) and physiological determinants of avian circadian rhythms (see a brief review in Meier and Russo 1985), as well as social factors (Moriarty 1977) to properly assess the tendency for parrots to join flocks through the day.

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MARCO AURÉLIO PIZO, ISAAC SIMÃO, *Dept. de Zoologia-I.B., Univ. Estadual de Campinas, CP 6109, CEP 13083-970, Campinas-SP, Brasil;* AND MAURO GALETTI, *Wildlife Research Group, Dept. of Anatomy, Univ. of Cambridge, Cambridge CB2 3DY, UK.* *Received 7 May 1996, accepted 10 Oct. 1996.*

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Male-biased breeding ground fidelity and longevity in American Golden-Plovers.— The American Golden-Plover (*Pluvialis dominicus*) and its close relative the Pacific Golden-Plover (*P. fulva*) are seasonally monogamous with both parents sharing in defense of the breeding territory, incubation, and care of the young (for a detailed treatment of breeding

biology in these species, see Johnson and Connors 1996). Previous studies of *fulva* showed strong male-biased site fidelity on breeding grounds in western Alaska, with marked females usually not seen after the season of banding (Johnson et al. 1993). We now report similar findings for *dominicus* in the same region.

Study area and methods.—Work was conducted from 1988 to 1996 northwest of Nome, Alaska on a study site of about 550 ha near the Feather River (at mile 37 on the Nome-Teller Road; Lat. 64°51′N, Long. 166°05′W). Connors et al. (1993) further describe the area. We captured 10 males and 10 females in nest traps, including both members of the pair in eight instances, and marked each bird with a unique combination of color bands plus a USF&WS metal band. A small survey flag was set at 12 paces from each nest to facilitate finding nests within and between seasons.

Almost all of the data presented here were collected during annual 2–4 week periods of field work in the following years (numbers of birds banded shown in parentheses): 1988 (2m, 2f), 1989 (1m, 1f), 1991 (none), 1993 (7m, 7f) and 1994 (none). In those years, we arrived on the site in late May–early June coincident with egg laying and the beginning of incubation (i.e., before nest loss and possible disappearance of marked birds was a major concern). This variable became significant in 1990, 1992, 1995, and 1996 when workers did not arrive at Feather River until after mid-June. Accordingly, only a few observations from these delayed arrival years are included.

We spent most of our time each year on the study site, and there is little question that all plovers in the area were found and observed. It was usually easy to locate site-faithful banded males in subsequent seasons. Distraction displays and defensive behaviors were focused near the previous season's nest within a relatively small portion of the much larger territory (the latter range from about 10–50 ha, Johnson and Connors 1996). To expand the hunt for missing birds, we searched (several times/season) a 1–2 km wide band of tundra surrounding the perimeter of the study area.

Results and discussion.—Gender-related breeding ground fidelity varies interspecifically among shorebirds. Little or no difference between sexes has been reported in some species; in others, males are clearly more site-faithful than females (see Johnson et al. 1993, Tomkovich and Soloviev 1994, Moitoret et al. 1996, Paton and Edwards 1996 for additional information and references). We found male American Golden-Plovers faithful to specific breeding territories with 8 of 10 observed near previous nests in seasons subsequent to banding (four/one season; three/three seasons; one/seven seasons). Conversely, none of 10 females were seen anywhere in or around the study area after the season of banding. Additional evidence of male-biased fidelity in *dominicus* (4 of 7 males and 0 of 2 females returned) was reported from breeding grounds on the North Slope of Alaska near Prudhoe Bay (Moitoret et al. 1996).

In postbanding years, four of the eight males from marked pairs had unbanded partners, two were apparently unmated, and two were missing from the study site. Altogether, we found seven nests of banded males in reoccupied territories. Of these, three nests were within 100 m of the nest where the male had been banded in a previous season, two males had moved about 250–300 m, and one male used the same nest cup in 1995 and 1996. Over the years, there were five instances (involving four banded males) in which the male reoccupied his usual territory together with an unbanded female, but no nest was found and neither bird showed nest-related alarm behaviors. After frequent observations of these pairs, we concluded that their clutches probably had been lost to predators.

Our findings from male and female *dominicus* are very similar to earlier studies of *fulva* (8 of 8 males and 1 of 4 females found in postbanding years, Johnson et al. 1993), and support Greenwood's (1980) hypothesis that "partitioning of resources by males prior to selection of mates by females should result in female dispersal." Either chance mortality of

sample females or natural mortality exceeding that of males could be misinterpreted as dispersal. That the former produced our results (80% of males found vs 0% of females found) is statistically very unlikely (P = .0004, by Fisher's Exact Test). Although natural mortality of *dominicus* has not been studied, we suspect that it is similar to *fulva* where there was no significant difference between the sexes in survival of color-banded birds on wintering grounds (Johnson et al. 1993).

We conclude that both of these plovers have a breeding system in which it is advantageous for males to reoccupy specific territories, and for females to disperse rather than seek previous partners. The male establishes the territory and performs most defensive behaviors (Johnson and Connors 1996), thus familiarity with a particular place should facilitate rapid reestablishment of territorial boundaries in early spring and effective defense during the nesting cycle. The benefits of site fidelity for males may be reduced in some seasons when delayed snow-melt lessens the attractiveness of a male and his territory. It is reasonable to consider lack of fidelity in females as an adaptation to variable spring weather whereby females pair opportunistically with males possessing suitable territories (Tomkovich and Soloviev 1994).

Interannual absence of marked females on our relatively large study site and surrounding area indicates dispersal over considerable distances. An occasional marked *dominicus* female might turn up at Feather River (as in *fulva*, Johnson et al. 1993). Despite lack of fidelity to a particular territory, females may have regional affinity on the breeding range.

Among other species, older birds and successful breeders tend to be the most site-faithful (for references, see Paton and Edwards 1996). How these factors affect *dominicus* is uncertain. Some of the birds banded were probably first-year individuals, but without reliable age criteria (Johnson and Connors 1996), we were unable to identify them. Because of unavoidable year-to-year variations in the scheduling of field work, we have only partial knowledge of breeding success as measured by successful hatching. Altogether, we monitored 18 nests (those on which birds were captured, plus nests in subsequent years). Of these, six clutches hatched, five were destroyed by predators, one was deserted, and six were still being incubated when field work ended. It is reasonable to include the five pairs without nests (see above) as indicators of predation; therefore at least 10 of 23 clutches (43.5%) were taken by predators. Most of these losses occurred early in the season and were probably first nesting attempts, a few may have been replacement clutches (Johnson and Connors 1996). Although we lack conclusive findings on the relationship between fate of clutch and subsequent male fidelity, our records suggest that lost clutches did not lessen interseason site-faithfulness of males.

Over the years, there were five cases (each a different bird) where males reoccupied their previous territories but were unmated. These lone individuals were observed repeatedly as we worked on the study area. Possible explanations for lack of a nest and female include: failure to attract a female (snow may have been a factor as mentioned above), loss of eggs followed by desertion of the female, delayed pairing (perhaps some pairs formed later in the season after our departure from Feather River), death of the female. The one record of nest desertion involved a male who incubated for at least two days (no female was observed during this time) and then abandoned the eggs. In this species, partners exchange incubation duties about every 12 h, giving the off-nest bird time to feed (Johnson and Connors 1996). Desertion seems inevitable if a mate disappears and the normal daily cycle is disrupted.

We report here the first record of longevity in the American Golden-Plover. Our oldest male was captured in 1989, and has returned to the same breeding territory through 1996. Assuming this plover was in its second calendar year when banded, the bird was at least eight years old in summer 1996. Maximum life span in this species probably exceeds 15 years as in the Pacific Golden-Plover (Johnson and Connors 1996).

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OSCAR W. JOHNSON, PATRICIA M. JOHNSON, *Dept. of Biology, Montana State Univ., Bozeman, Montana 59717;* PHILLIP L. BRUNER, ANDREA E. BRUNER, *Dept. of Biology, Brigham Young Univ.–Hawaii, Laie, Hawaii 96762*; RONALD J. KIENHOLZ, *210 7th St. N. E., Dilworth, Minnesota 56529*; AND PAUL A. BRUSSEAU, *P.O. Box 142375, Anchorage, Alaska 99514.*
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Greater Flamingos breed on Aldabra Atoll, Republic of Seychelles.—A Greater Flamingo (*Phoenicopterus ruber roseus*) chick was observed on 13 April 1995 on Aldabra Atoll, Republic of Seychelles (46°20′E, 9°24′S). The chick was in a brackish tidal basin located in the Cinq Cases/Takamaka region of the island of Grande Terre. The basin is approximately 1.1 km^2 in area and is 700 m from the coast and 1500 m from the lagoon. Two adults were with the chick, although as many as 19 flamingos were in the same basin earlier in the year. The chick was one-third to one-half adult-size with dark gray legs and decurved bill and covered with gray down. It probably was between 25 and 39 days old (Uys et al. 1963). We found three complete nests and three incomplete nests in the basin, but only one nest appeared to have been used. The nests were short cylindrical pillars of mud with a shallow concave nest cup. We took measurements of the single used nest: total height was 33.5 cm, nest diameter was 32.5 cm × 38 cm, nest cup diameter was 13.5 cm × 18 cm, and nest cup depth was about 2.5 cm. All six nests were clumped together

approximately 30 m from shore and 5 m from a small clump of mangroves (*Avicennia marina*). The nests were in 8.5 cm of water at the time of discovery, but due to tidal influences the height of the nest above the apparent high water mark was 12 cm. The juvenile was observed two months later at the same basin on 15 June with two adults. One of the adults took flight, circled the basin three times, and landed. The juvenile then took flight, circled the basin twice, and landed after approximately 10 minutes in the air. This was probably one of its first flights as the young first fly 70–90 days after hatching (Cézilly et al. 1994). The juvenile was last observed with 15 adults at Bassin Flamant on 12 September. Bassin Flamant is approximately 3 km from its natal basin.

There are no previous known records of flamingos successfully breeding on Aldabra (Benson 1984), despite a reference that flamingos breed on Aldabra in small numbers (Feare and Watson 1984). A single fresh egg was found at Grand Bassin Takamaka on 25 September 1967 by Benson and Penny (1971) after a single flamingo had flown away, but no nest mound was found and this was not accepted as evidence of breeding (Benson and Penny 1971, Benson 1984).

Whether flamingos on Aldabra are a resident population or a migrant population from East Africa has been speculated for some time. If it is a migrant population, it is odd that flamingos have not been sighted on other nearby islands such as Cosmoledo (Penny 1974). The apparent absence of flamingos in the winter months of May–Aug. is probably a result of the lack of observers rather than migrating flamingos, as birds were seen from June–Sept. 1995 when research officers were present on Aldabra. Flamingo numbers have also appeared to decline since first being described at the turn of the century when Abbott estimated between 500–1000 flamingos and Dupont recorded "several hundreds" (Benson 1967). In 1964–1965, Gaymer (1967) estimated there were about 50 flamingos on Aldabra, while the highest number of flamingos recorded at any one time in 1967–1968 was 55 (Benson and Penny 1971). The greatest number of flamingos observed at one time between Dec. 1993–April 1994 was 32; the greatest number between Nov. 1994–May 1995 was 24; and the greatest number between April 1995–Nov. 1995 was 28. The evidence seems to support that flamingos on Aldabra are residents, but whether they constitute a breeding population or represent a "dead end" for a group of birds that wandered to Aldabra is still unknown.

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RAYMOND E. RAINBOLT AND DAVE M. AUGERI, *Dept. of Fisheries and Wildlife, 104 Nash Hall, Oregon State Univ., Corvallis, Oregon 97331;* SUSAN M. PIERCE, *2408 23rd Ave., Greeley, Colorado 80631;* AND MITCHELL T. BERGESON, *E9599 State Rd. 40, Colfax, Wisconsin 54730.* *Received 15 Aug. 1996, accepted 15 Oct. 1996.*

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Wildlife mortality and entanglement by discarded hip chain string.—The assessment and quantification of an organism's habitat is essential in accomplishing many research and management goals. A component of this is the measurement of linear distances, occasionally over many kilometers (Gysel, L. W. and L. J. Lyon. 1980. Habitat analysis and evaluation. Pp. 305–327 *in* Wildlife management techniques manual [S. D. Schemnitz, ed.]. Fourth ed. The Wildl. Soc., Washington, D.C.; Orth, D. J. 1983. Aquatic habitat measurements. Pp. 61–84 *in* Fisheries techniques [L. A. Nielsen, and D. L. Johnson, eds.]. Am. Fish. Soc., Bethesda, Maryland). Hip chains (also called string boxes) are a valuable tool used by biologists to measure long distances where using a tape measure would be difficult, if not prohibitive. Hip chains meter a polyester or cotton string that is pulled from a spool inside the unit. The observer ties the string to a stationary object and walks away as the hip chain tallies the distance traveled on an odometer. Hip chains have the advantages of allowing the observer to measure distances while both hands are free to complete other tasks and the string is advertised as disposable (e.g., 1996 Ben Meadows Company catalog). However, the string left behind can be an eyesore or a source of mortality for wildlife as this article demonstrates.

In May, 1994, I used a hip chain to measure linear stream distances in the Oregon Coast Range, Lincoln Co. I used cotton (biodegradable) string and walked within the stream's wetted channel. Nine days later, I walked the same stream and found a dead American Dipper (*Cinclus mexicanus*) tangled in the residual string (Fig. 1). The string left behind was still in long (>100 m) segments, had floated downstream, and had accumulated on the upstream side of rocks and woody debris. The dipper's legs were greatly entangled in the many loops formed in one of these accumulations. These loops appeared to have tightened as the bird struggled or was swept downstream and the bird was unable to escape.

Discarded hip chain string also has killed other wildlife. I informally surveyed colleagues locally and queried subscribers to electronic bulletin boards dedicated to wildlife topics. Nineteen respondents reported ≥13 species of which >24 individuals were dead and 9 individuals were released alive. Animals killed were 4 bats, 5 Western Screech-Owls (*Otus kennicotti*), 4 Northern Spotted Owls (*Strix occidentalis caurina*), >3 unidentified songbirds, 2 thrushes, 2 American Robins (*Turdus migratorius*), 2 Varied Thrushes (*Ixoreus naevius*), a Wood Thrush (*Hylocichla mustelina*), Belted Kingfisher (*Ceryle alcyon*), and a Steller's Jay (*Cyanocitta stelleri*). Two robins, and a Red-tailed Hawk (*Buteo jamaicensis*), Long-eared Owl (*Asio otus*), Northern Saw-whet Owl (*Aegolius acadicus*), Spotted Owl, Western Screech-Owl, Flammulated Owl (*Otus flammeolus*), and Northern Pygmy-Owl (*Glaucidium gnoma*) were found entangled and released alive. Most animals (>93%, N = 32) were caught in flight, 1–1.5 m above the ground or water. Few (25%) were snared only by the tip of one wing with two to five wraps of string; however, the rest were completely tangled, indicating they struggled to free themselves following capture. The Spotted Owls were all caught in thicker cruising string whereas all others were tangled in hip chain string. Animals

FIG. 1. Adult American Dipper found dead entangled in discarded hip chain string in the South Fork of Drift Creek, central Oregon Coast Range, May 1994.

were captured over a stream (47%) and in the upland (53%, n = 32). Hip chain string is potentially lethal immediately and remains so for a considerable time period. Animals were found <2 h to 5 years following string deployment (median = 11.5 days, N = 22). Marketing of new "stronger, long-lasting polyester thread!" may extend the potential for mortality to wildlife, although five respondents reported no qualitative reduction of the strength of the "biodegradable" cotton string after >1–2 years of exposure. Animals were captured throughout the U.S. (Alaska, Arizona, California, Idaho, Massachusetts, North Carolina, Oregon, Vermont, and Washington) and Canada (British Columbia, New Brunswick, and Nova Scotia).

Discarded string from hip chains pose an added risk of entanglement and mortality to terrestrial and aquatic organisms, regardless of the string's biodegradability. Nocturnal flyers (owls and bats) appear to be particularly susceptible. It is possible that this string could entangle fish and amphibians as well. Therefore, I recommend that biologists and foresters use hip chains with caution. Alternatives to reduce this hazard include recovering the string

immediately after use (≤24 h), using a visual estimation technique that corrects for bias (e.g., Hankin, D. G. and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Can. J. Fish. Aquat. Sci. 45:834–844), deploying string at ground level (<0.1 m), or in aquatic systems, walking on the stream bank where it is unlikely that a large volume of discarded string will be accumulated by the stream. Hip chains are a valuable tool; however, their widespread use and persistent threat necessitate additional precautions to reduce incidental wildlife mortality.

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John P. Loegering, *Oregon Cooperative Wildlife Research Unit, Dept. of Fisheries and Wildlife Science, Oregon State Univ., Corvallis, Oregon 97331-3803.* *Received 29 Aug. 1996, accepted 12 Nov. 1996.*

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ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

A Photographic Guide to North American Raptors. By Brian K. Wheeler and William S. Clark, Academic Press, London, UK, 1995, 198 pp, 377 color photographs $39.95 (cloth).—This new raptor guide presents sizable color photographs of every recognizably different plumage (age, sex, race, and color morph) of every species of diurnal raptor that regularly occurs in North America, as well as representative plumages of documented vagrants. The majority of the color photographs were taken by Wheeler, with a lesser number by Clark and selected photos from other sources. The outstanding selection of photos reveals the efforts the authors made to clearly document all the field marks on film.

The elegantly succinct species accounts begin with a description of key field characters for each plumage, followed by a listing of similar species, the field marks by which to differentiate them, and references to photos of similar species in similar attitudes elsewhere in the guide. A series of usually dazzling photographs follows, ranging from three for the California Condor (*Gymnogyps californianus*) to forty-six of the highly varied plumages of Red-tailed Hawk (*Buteo jamaicensis*). With few exceptions, species accounts include shots of birds perched and in flight (usually from below). A summary of evident field marks accompanies each photo, often referring the reader to comparable photos of similar species.

The guide concludes with a special section of fourteen "Raptor Identification Problems" in which photos of confusing species in approximately the same attitude are juxtaposed to help resolve difficult identification problems. Topics range from differentiating Sharp-shinned Hawk (*Accipiter striatus*) and Cooper's Hawk (*A. coopereii*) to "Pale square primary panels on upperwings of flying buteos."

The photographic guide is best understood with reference to the "Field Guide to Hawks" (1987) by Clark and Wheeler. The photo guide complements rather than replaces "Hawks" which remains the most extensive guide to North America's diurnal raptors. Wheeler's expert illustrations in the field guide present an assortment of diverse plumages not previously conveyed in any North American guides, and Clark's text provides a wealth of insight and technical detail not available in any other source. "Hawks," however, includes 242 black-and-white photographs that are quite small and have lost much of their clarity in reproduction and, therefore, are of limited value to the reader.

The new guide is, in one sense, an amplification on the photo section in "Hawks," but it is also much more than that. The photos are much larger than in "Hawks," and the overall quality of the selection and their reproduction are vastly superior. Quite simply, this is a beautiful book, worth the price for the spectacular raptor photography alone.

The text and photo captions are elegant in their simplicity and clarity, essentially referring only to those field marks that are documented photographically. Wheeler and Clark intentionally avoid discussion of the more esoteric subject of "jizz." (See Dunne, Sibley, and Sutton, "Hawks in Flight." 1988.)

The photo guide does not attempt to provide the wealth of information on each species available in "Hawks," such as descriptions of flight, behavior, status and distribution, fine points, unusual plumages, etymology, and range maps. Although the plumage descriptions in "Hawks" are also more extensive than in the photo guide, the latter offers insightful new field marks for some species, such as juvenile Red-tailed Hawks.

The photo guide also provides new data on the range of length, weight, and wingspan for each species, based solely on direct measurements of live birds and specimens. The

authors eschew all published sources (some of which were used in "Hawks") in the belief that some of the previously published data are erroneous.

The only downside of the guide's relatively large size (25 cm × 16.5 cm) is that it is not easily carried in the field. However, most hawk watchers will want one in the field, no matter how much of a beating it might take, and one at home, as with the field guide. (The publishers should be commended for providing a beautiful yet rugged cover, able to tolerate typical field abuse.)

There are very few errors in the book—basically very minor proofreading oversights. In the topography of a hawk, the terms for axillaries and breast are reversed, and in one reference, White-tailed Hawk (*Buteo albicaudatus*) is identified as White-backed. Some mistakes are evident in the photographic cross references, especially in the "Raptor Identification Problems," suggesting a late change in photo sequence (e.g., Photo FH05 should refer to RL10, not RL09. and FH11 should refer to RL18 & RL19, not RL17 & RL18). Also, the scientific names for Hook-billed Kite (*Chondrohierax uncinatus*), Zone-tailed Hawk (*Buteo albonotatus*), and Red-backed Buzzard (*Buteo polyosoma*) contain minor typographical errors.

Wheeler and Clark have, in the field and photographic guides, performed an invaluable service for everyone interested in hawks. Quite simply, there is nothing like either book for North America's diurnal raptors. You can use either book separately, but anyone seriously interested in hawks clearly should use both.

"A Photographic Guide to North American Raptors" establishes a new, very high standard, not only for raptor identification but for all photographic field guides.—PAUL M. ROBERTS.

THE BIRDS OF ISRAEL. By Hadoram Shirihai (E. Dovrat and D. A. Christie, editors). Academic Press, London and San Diego, 1996: xc + 692 pp., 96 composite photographic color plates (1–11 photographs per plate), 200 + line drawings, ca. 1000 maps, gazetteer. $99.00.—In a normal book review, the quality of the text and of the illustrations receive most of the reviewer's attention. In the case of "The Birds of Israel," however, I must say that in more than four decades of reviewing I have never handled a book so poorly made. It weighs 8 lb (3.64 kg), and the text alone is slightly more than 2 in (5 cm) thick. The binding (thin cloth over cardboard) is utterly inadequate to hold together a book of this size. After a minimum of handling, the front and back endpages of the review copy, a single double-width sheet each, are all that is holding the text to the binding, and these have begun to rip away.

Was a book of this size necessary to present all of the included information? By no means. It is printed on a fairly heavy coated stock; a slightly lighter-weight paper might have sufficed. Perhaps more importantly, there is much wasted space in the text. The headings of the species accounts are in 14-point type and those of the family accounts in 16-point. The text is a mixture of one-/and two-column formats. There is much white space on the pages, especially around some of the maps and line drawings.

The line drawings by Alan Harris are attractive, but are an unnecessary luxury in a book of this kind and size. Furthermore, the spot drawings in the introductory pages are not identified: Stone-curlew, p. xxiv; Alpine Accentor, p. xxxviii; Hen Harrier, p. xliii; Hawfinch, p. xliv; Ruppell's Warbler, p. xlv; White Stork, p. liv; Black-crowned Night-Heron, p. lv; two subspecies of Redstart, p. lvi; Brown Booby, p. lx; Black-headed Plover, p. lxi; Black-shouldered Kite, p. lxii. Most of the drawings capture the Gestalt of the species reasonably well, but errors in bill length and shape are easily detected by looking at those drawings

for which a photograph is also supplied (see particularly the Pied Kingfisher drawing on p. 338).

There are two sets of color photographs. The first 12 plates show species typical of various seasonalities of breeding birds and of migrant and wintering birds, plus vagrants arranged by their geographic origins. Plates 13–24 illustrate habitats in Israel. Later in the book comes a series of 72 plates, mostly composite, of birds with "an emphasis . . . placed on the more important and most attractive species in Israel." The definition of "important" must include vagrants, as the very first photograph in this series portrays the first Western Palearctic record for Streaked Shearwater. Incredibly, there are no cross-references on the plates nor in the species accounts; the only way to find a photograph of a given species is to look in the index entry for that species. Similarly, to find the text reference for a photographed species it is also necessary to turn to the index.

The systematic sequence in the species accounts is essentially that of Voous, published in The Ibis in 1973 and 1977. Although still used in a few European publications, this sequence is little known to Americans, and as a result families are not always where you might expect them (i.e., the Corvidae are in the middle of the Passeriformes, not at the end or near the beginning).

There are nearly 100 pages of introductory matter; in addition to the expected Foreword, Preface, and Acknowledgements, there is a "General Introduction," within which there is a history of ornithology in Israel (beginning with species mentioned in the Bible), and a section on "The main features of the Israeli Avifauna," with separate chapters on the breeding, wintering and migrant species, plus vagrants. Then comes a "Relevant (!) Introduction," including explanations of the layout of the species accounts, maps and symbols. There is a very detailed (12 pp) description of the climate, vegetation, geology, and other factors influencing bird distribution in Israel.

Then come the species accounts. The current and original scientific names are given, the latter with author and date but not full citation. A short paragraph summarizes the world and Middle Eastern distributions of the species, and a similar paragraph serves for the subspecies (one or more) in Israel. A paragraph on "Status, habitat & general occurrence" is set in a larger typeface than elsewhere in the species account. This paragraph and those above it run across the page; the remainder of the species account is in two-column format. The main headings are "Distribution, numbers & annual cycle" and (when pertinent) "Subspecific identification." Under the first of these, there are (again, when appropriate) separate paragraphs for autumn, spring, winter, and summer, plus a parenthetical paragraph on the status of the species in the Sinai. Data in these paragraphs are presented in overwhelming detail, often giving estimated daily maxima at a series of localities. "Subspecific identification" clearly refers to birds in the hand, and will be of use only to banders and for identification of salvaged dead birds.

There are several kinds of maps, as many as 3, within the species accounts. Although there is a 3-page section defining the symbols and conventions employed in the maps, one looks in vain for any sample maps to show how these are actually used in practice. There is a map of Israel on the end pages and within the text, but (not surprisingly) it shows very few of the ca. 800 localities listed in the Gazetteer. Latitude and longitude, as well as the "nearest town" (which is not necessarily one shown on the book's map) are given in the gazetteer, but after having tried to locate a number of places, I can state that a large-scale folding map would have been a major asset to this book.

Without having read all of the species accounts thoroughly, I found some small flaws, and there are no doubt others. For example, the Horned Grebe (*Podiceps auritus*) is not monotypic; a general discussion of vagrancy in seabirds is appended to the species account for the Shy Albatross; the subspecies account for Leach's Storm-Petrel (*Oceanodroma leu-*

corhoa) is erroneous (the nominate race is said to breed "throughout species' range except in North America, where a different subspecies occurs"). On p. 265 there are tables of characters differentiating various taxa in the Herring Gull complex (primary pattern of adults, pattern differences in wings and tail of juveniles), but the *striking* differences in leg and bill colors are buried in the text; I was able long after the fact to identify a bird I saw in Israel as the Armenian Gull (*L. armenicus*) but only by using other reference works. A statement of the relative abundance of the black-/and white-throated morphs (a geographically variable phenomenon) of the Black-eared Wheatear (*Oenanthe hispanica*) would have been of interest; we saw about 10 on Mount Hermon on 4 April 1986, only one of which was of the white-throated morph.

There is an appendix in four parts. First are five species recorded exclusively in Sinai; then "Species reported in Israel and under review"; then "Records previously published, but species' occurrence in Israel and/or Sinai subsequently rejected"; and then "Escaped cagebird species." In the second list, Shirihai is tough on sight records, even his own (see Socotra Cormorant [*Phalacrocorax nigrogularis*]). This list also includes records of *collected* birds, with the species placed on hold because the specimen(s) cannot now be found. The difference between the second and third lists is not always clear—in several instances species are admitted to the second list on the basis of sight records, followed by "No documentation," and other sight records are relegated to the third list and said to be "unsubstantiated." Some published records are said to be "unacceptable" or "rejected," but seldom are we told why.

I spent 1–16 April 1986 in Israel on a tour with a highly competent and knowledgeable leader, Mark van Beirs; we covered virtually the entire country from Mount Hermon to Eilat. Judging from the status as given in "The birds of Israel," some of our observations were noteworthy.

Dalmatian Pelican (*Pelecanus crispus*). Shirihai accepted only seven records of this rare winter visitor in Israel, with dates ranging from 13 October to 7 April. We saw one on 2 April, in a flock of ca 70 Great White Pelicans (*P. onocrotalus*) soaring over the intersection at the turnoff for Kefar Blum in northern Israel. It was easily recognizeable by its lack of jet black on the undersides of the remiges.

Yellow Wagtail (*Motacilla flava*). Shirihai states that the migration of *M. f. feldegg* at Eilat is "mainly mid February to end March." There were two *feldegg* and eight *beema* on a football field at Eilat on 14 April, and a flock of over 100, including both subspecies, in the northern fields of Eilat on 15 April.

Rock Thrush (*Monticola saxatilis*). According to Shirihai, the resident population of this species on Mount Hermon arrives during the second and third weeks of April. We saw six males on Mount Hermon on 4 April; these may have been migrants of another population.

Marsh Warbler (*Acrocephalus palustris*). Shirihai considered this species "very rare to mid-April." We saw 2 on 5 April in bushes near the water's edge at the mouth of the Jordan River at the north end of the Sea of Galillee.

Common Raven (*Corvus corax*). Two or three pairs of this species are said to be resident in the central Negev between Sede Boqer and Mizpe Ramon. We saw a pair on 10 April in a canyon at En Avedat within this area.

Finally, an addition to Shirihai's list of escaped cagebirds—an oddly familiar call led me to a dark blue and white Budgerigar (*Melopsittacus undulatus*) in the date palm grove just east of the salt ponds at Eilat on 15 April.

For an Israeli perspective on Shirihai's book, I recommend the incisive review by Yoram Yom-Tov (1996. Ibis 138:589–590). He summarizes his review by stating "in the Introduction this book provides good information on bird life in Israel and is a good source of information on the taxonomy, distribution, movements and migration of the birds of Israel.

However, it fails to fulfill its promise and does not constitute a comprehensive review of the present ornithological knowledge in Israel. It is unfortunate that, owing to the abovementioned failures, most quantitative parts of the book [of which there are very many] are of little scientific use."

For most readers, an adequately comprehensive account of the Israeli avifauna can be found in "The birds of Israel" by Uzi Paz (Christopher Helm, London, 1987) which weighs only about two pounds! Its 29 line/scratchboard drawings by Chris Rose are at least as attractive as those of Alan Harris in the book under review, and there are 60 color photographs, only two of which are reproduced at less than half-page size, unlike many of those in the Shirihai book. Unfortunately the Paz book appears to be out of print, but it's worth searching for as an alternative to Shirihai's gargantuan tome.—KENNETH C. PARKES.

ATLAS SAISONNIER DES OISEAUX DU QUÉBEC. By André Cyr and Jacques Larivée. Presses de l'Université de Sherbrooke et Société de Loisir Ornithologique de l'Estrie, Sherbrooke. 1995: 711 pp., 37 numbered text figs., numerous line drawings, over 1100 distribution maps, 3 transparent overlays; US$ 56.95 (paper). [Available from "Société de Loisir Ornithologique de l'Estrie, a/s Atlas saisonnier, C.P. 1263, Sherbrooke (Québec), Canada J1H5L7."].—Quite clearly, this new atlas, illustrating the seasonal distribution of over three hundred species of birds in Québec Province, Canada, is a splendid achievement that deserves wide recognition in North American ornithology in general and biogeography in particular. What I found impressive about it are the huge data base upon which it rests, the well thought-out methodology of data capture and subsequent data reduction to produce meaningful and easily understood cartography, and in general, the vast amount of useful distributional information, whether in the form of maps or of text, contained between its covers. Before describing this volume in detail, I wish to congratulate all the ornithologists in Québec who over the years have amassed such a wealth of observation points, the twelve authors of species accounts (listed below), and especially the Atlas's two main authors, André Cyr and Jacques Larivée, for a job well done.

The "Atlas saisonnier" treats 303 species of birds occurring in *southern* Québec Province ("Québec méridional"; see Figs. 2–9, pp. 4–9). By southern Québec is meant "the portion of Québecois territory located south of 52°N latitude" (p. 4). The Atlas's title is thus misleading: why is it not "Atlas saisonnier des oiseaux du Québec méridional"? The book is based on data points accumulated by numerous ornithologists during the period 1969–1989. The raw data used to compile the atlas are a total of 128,076 daily observation protocols ("feuillets d'observations quotidiennes"; sample on p. 12) filed by field observers, an average of 6099 protocols per year. All these field workers are members of the clubs of the "Association québecoise des groupes d' ornithologues." "Nearly 72% of the territory of [southern Québec] south of 50°N was covered by this study" (p. viii). This huge data base (ÉPOP = Étude des populations d'oiseaux du Québec) has been treated by computer analyses to produce four seasonal distribution maps for each of the 303 species, one each for the spring (1 Mar.–30 Apr.), summer (1 May–31 July), fall (1 Aug.–30 Nov.), and winter (1 December–29 February) seasons. The subdivision of the year into these four seasons is clearly explained on pp. 15–17. Each map presents a certain number of rectangles encompassing a surface area of 10 minutes of latitude and 12 minutes of longitude. Three different tones of shading (besides white-absence of the species) indicate a scale of relative local frequency in each rectangle.

A detailed introductory section (pp. 1–10), describing the various features of the area covered by the atlas, is followed by a section on methods (pp. 11–33), a section on spatio-

temporal distribution of birds in southern Québec (pp. 34–43), and a section on the distribution of biodiversity in southern Québec (pp. 44–52). This last section is of special interest in terms of conservation in the region. This analysis emphasizes the dual aspect of species diversity (p. 52). One aspect reflects the concept that one ought to protect regions having the highest number of species, whereas the second aspect underlines the concept that one should preserve areas with threatened or endangered species and those areas where the highest number of geographically restricted species occur. This is similar to what some biogeographers would call areas of endemism, although this term is not used in the Atlas.

As Larivée made clear in his summary (p. viii), an atlas like this one can help the user answer many kinds of questions. Such queries include where each species is found at each season, how many species can be found at each season, what species have increased or decreased in their distribution area, and how much surface area does a particular species occupy. All these questions, and many others, are listed, and the reader is told where answers can be found (whether on range maps or in the text, tables, or appendixes) in a convenient table on p. 53. Because the maps synthesize many data points and represent a summary of relatively complicated methods of raw data analysis, they are not necessarily easy to "read." This potential difficulty is remedied by the clear instructions presented on p. 54.

The most substantial part of the atlas, pp. 56–661, includes the accounts of the 303 species treated, from Red-throated Loon (*Gavia stellata*), (pp. 56–57) to House Sparrow (*Passer domesticus*) (pp. 660–661). This is followed by 10 Appendixes (pp. 662–691), a list of references (pp. 695–705), an index to the French and Latin names of birds (pp. 706–711), and three pages of transparent overlays, which reproduce Figs. 3–9 given in the introductory section and which can be conveniently detached if one needs to superimpose them on the species' distribution maps.

The format of the double-page species accounts is uniform throughout the atlas, hence interspecific cross comparisons are quite easy to make. On the left page are the text, a line drawing, and a table indicating the seasonal occurrence of the species treated. The French, Latin, and English names of the species are given. The text deals with seasonal status, area and habitat occupied, and biogeographical "faunal type" (defined in the Glossary, p. 694, and more explicitly on p. 31: "Faunal type represents a biogeographic region characterizing the whole of the world distribution of the species"). The text of each species account is signed by one or two of the following twelve authors: André Cyr, Philippe Fragnier, Marc Gauthier, Serge Gauthier, Michel Gosselin, Christian Houle, Diane Lacombe, Denis Lepage, Michel Robert, François Schaffer, Julie Schaffer, and Marc-André Villard. These texts are compact and succinct, yet much information is packed into them. I regret, however, that brief English summaries were not included: they would have added immensely to the usefulness and value of the Atlas. On the right page of each species account are the four seasonal maps. For some species, however (for example Greater Shearwater [*Puffinus gravis*], Sooty Shearwater [*P. griseus*], and Manx Shearwater [*P. puffinus*], there are only two maps, as the species in question occur only during two of the four seasons identified in the atlas.

One outstanding aspect of this atlas is the seasonal maps. Thus it is possible to visualize the seasonal status of over 300 species of birds at a glance, a very useful feature indeed. As I wrote at the beginning of this review, I am very impressed by this Atlas. Nevertheless, given the vast amount of work that went into the development of this project, from the field work to the data capture, the computer treatment, and the final production of the book, it seems to me that it would have taken only a few extra steps to include a few extra items that would have made the volume even more useful to an even broader audience. I have already mentioned the somewhat misleading title and the lack of English summaries in the species accounts. I am sorry that the Latin names of the plant species mentioned in the description of vegetation types (p. 9) are not given (who among even a French-reading, but

non-French Canadian user, will know what "épinette noire" or "caryer" are?). Similarly, English-language equivalents of the vegetation types should have been indicated. I was also disturbed by the fact that the species names in the long—and very useful—Appendices 1–7 are only in French. Why were the Latin names not included, thus making the use of these tables even wider? I am sorry that a line drawing of each species was included in the text. Some of these sketches are fine, but many, I regret to say, are rather mediocre. Whether attractive or not, these line drawings add nothing to the book. Instead, they use up precious text space that would have been better utilized by including additional distributional information. In any case, illustrations of all these birds can be found in one or more of the several North American field guides now on the market. The use of the transparent overlays (especially overlays B and C) would be greatly increased had the lettering included also an English language version (or else had two parallel overlays been published, one in French and a second in English). And last, but in some ways not least, of my criticisms, are the size, cover, and paper of this atlas. Let me say here that I love atlases. Right next to my computer on my book shelf are my favorite atlases which I use daily. Some are purely geographic, others are more thematic, such as the bird atlases. I find the atlas format one of the most rewarding ways of presenting some kinds of information. The point I am making here is that to be fully useful a good atlas must not only include well presented information but it must also be of a size and printed on paper and bound in such a way as to be a craftsman's tool. Whereas the Atlas saisonnier is a great piece of work that contains a mass of invaluable information, it fails on the other score. It is wider (28 cm) than high (22 cm) (just the opposite of most atlases), it has a very soft and slippery paper cover, and its paper is almost Bible-thin, so that the printing is visible through the page. Together these three qualities make this book a very awkward volume to use. Because of the weak cover and thin paper it "flops" uncomfortably. Because the unit of study and presentation in the atlas is the species entry on a double-page, the effective size becomes even wider. Whereas this might seem like a trivial point, in fact it is not. Again and again, I found it difficult to scan from text to maps because of the size involved, encompassing a total width of over 50 cm. Even if it were rebound, for example in thick library-type cloth binding, its wider than high size would probably make its spine vulnerable to heavy use. If André Cyr and Jacques Larivée are thinking of ever updating their otherwise wonderful Atlas saisonnier and of publishing a new edition, I strongly urge them to re-think the size, binding, and paper.

Clearly, the Atlas saisonnier will be most useful to French-speaking Canadian ornithologists who reside in southern Québec Province. Next it will be useful to all ornithologists interested in the distribution patterns of birds along the Atlantic seaboard of North America. My criticisms aside, I highly recommend that this innovative new Atlas be studied by all avian biogeographers, whether from Canada, North America, or elsewhere.—François Vuilleumier.

Birds of Kenya and Northern Tanzania. By Dale A. Zimmerman, Donald A. Turner, and David J. Pearson. 1996. Princeton Univ. Press, Princeton, New Jersey. 740 pages, 112 color plates. $65.00 (cloth).—The east African region, Kenya in particular, is among the most heavily-visited ecotourism destinations in the world. Visitors long have chafed at the absence of a comprehensive modern guide to the region's birdlife. This much-awaited volume rectifies that problem with a nearly 2-kg thud. Covering 1080 species admitted by the authors to the Kenyan list as of December, 1994, plus 34 species found in adjacent northeastern Tanzania included at the urging of safari operators and others, this book addresses 1114 species with detailed text and lifelike, mostly color illustrations. For most, it gives thorough field and sometimes in-hand descriptions of major plumages (including downy young) and discusses geographic variation, voice, habits, similar species, and status and

distribution within the area of coverage. The local range of nearly all species is shown on small, black-and-white maps. Many of the 124 plates (112 in color), all grouped near the front of the book, have between twenty and thirty images, showing differences not only between species but also between sexes, ages, and populations within species. More than half were painted by Zimmerman before his eyesight deteriorated, when Ian Willis and Douglas Pratt stepped in to complete them. The opposite text mostly summarizes the status, range, and habitat of each species and often also gives a brief summary of field characters.

The book's relatively short introduction gives some of its rationale and explains how to use it, including a glossary of nearly 200 terms used in the text down to the level of mandibular ramus and zygodactyl. In the introduction also is a short section briefly synthesizing the region's geography and ecology, accompanied by 38 black-and-white photos of typical habitats and four keyed black-and-white maps showing major locations mentioned in the text. Following the species accounts are appendices listing those species found in Tanzania and Uganda not treated by this book, a gazetteer giving latitudes and longitudes for about 500 locations mentioned in the text, about 250 literature citations, and indices to English and scientific names.

"Birds of Kenya and Northern Tanzania" is a truly significant contribution to the body of ornithological knowledge of East Africa, and every serious student of its birdlife should own or have access to a copy. But, I also think interest in this book partly will reflect the absence of significant alternatives. It is less a field guide than a handbook and not a particularly "user-friendly" one at that. The species accounts and plates are so densely written and drawn that probably they will be difficult for many people to digest readily and use effectively. The maps, lacking reference points or color, often just giving spots where a species has been recorded, seem almost like wasted space, for few readers will be able to understand a species' range in the region covered without carefully referring to the text and gazetteer. That space might have been used instead to expand the discussion of the region's physiography and environment, for example, providing a better framework for understanding its often puzzling bird distribution. The authors claim that their systematics and nomenclature most closely follow the "Birds of Africa" series (Academic Press, 1982 ff), where available, rather than any other modern published work. I readily found deviations from that, or any, familiar standard, but most were at least explained, albeit with varying convincingness. Clearly Africa needs a unifying force for taxonomy and nomenclature. A rather unmodern practice of this book is to use trinomials widely, even on species headings when only one recognized subspecies occurs in the region covered.

Concerns such as mine are likely to be addressed in subsequent editions of "Birds of Kenya and Northern Tanzania," or by authors of other works in the future, as was the case following the publication of Roberts' pioneering "Birds of Southern Africa." For now we should be thankful that this massive undertaking has come to fruition, and that such a comprehensive reference guide is finally available for this popular destination. The authors state that their book is designed for use on safari, not for bookshelf decoration. I expect that potentially it will be most beneficial for general preparation before heading into the field, and for attempting to resolve particular field problems at the end of a field session or the day. In the field itself, I suspect most users will find it heavy, both literally and figurative.—P. WILLIAM SMITH.

THE MIGRATION OF KNOTS. By Theunis Piersma and Nick Davidson. Wader Study Bulletin 64, Supplement, April 1992 (Wader Study Group, P. O. Box 247, Tring, Herts. HP23 5SN, U.K.). Proceedings of a workshop on "Recent advances in understanding Knot migrations" held in Ribe, Denmark, 21–22 September, 1989: 209 pp., a color frontispiece with no cap-

tion, 28 papers divided into five sections, 26 b/w photographs, 41 maps, 28 tables, 67 figs., £15 (softcover) includes postage and packing.

THE FLIGHT OF THE RED KNOT. By Brian Harrington with Charles Flowers. W. W. Norton and Company, New York, London, 1996: 192 pp., 50 colour photographs, 8 maps. $29.95 (hard cover).—The work described by Piersma and Davidson in the Wader Study Group Supplement is divided into five sections with 28 papers by 32 authors from 14 countries on the migration dynamics of five subspecies of the Red Knot (*Calidris canutus*). This "supplement" is truly an international effort with papers by authors from Russia (1 paper), Norway (2), Iceland (2), Germany (1), Sweden (3), Denmark (2), Poland (2), Australia (1), South Africa (1), England (4), The Netherlands (7), France (1), Canada (4), and the United States (1). In their "introduction," Piersma and Davidson state that shorebird researchers "form enthusiatic and communicative flocks". The information exchanged between members of this flock from all the major flyways over a 20-year period resulted in the workshop and this volume. The main sections of this book describe (1) the origins, genetics and distribution of the subspecies, (2) the migration systems of four subspecies (the fifth *Calidris canutus roselaari*, hitherto unrecognized, is described for the first time in this volume), (3) *islandica* (western Europe) knots in spring and summer with five of twelve papers stressing the very important role of Iceland as a major staging area, (4) autumn and winter movements in Europe and Africa, and (5) a synthesis of the five subspecies in light of their migrations and annual cycles and an assessment of conservation needs and implications. It is an attractive volume with a colour photo of roosting/flying knots in the Dutch Wadden Sea on the 8″ × 12″ cover and 26 black-and-white photographs dispersed throughout.

The book does not address a specific problem (although a recent population decline appears to be of special interest to the editors) or attempt to answer a particular question. It describes all that is known (up to 1992) about the genetics, migration routes, continental population levels and aspects of body condition of a single species of shorebird on a worldwide basis, not an easy objective to accomplish for any species of migratory bird. But, as editors, Piersma and Davidson come as close to reaching this remarkable objective as anyone could hope for even though much information is still lacking (as identified throughout this volume).

Harrington's book was derived from a nature film entitled "Mystery of the Animal Pathfinders." It represents one man's fascination with a species and his determination to understand its movements across the hemisphere. Consequently, it covers two important topics: (1) the extensive migrations of a most interesting species of shorebird and (2) the work of Harrington, the "pathfinder." Unfortunately, I found the book to lack focus. But the reader must be especially aware that this reviewer is a scientist searching for scientific information, whereas a naturalist, interested in conservation issues dealing with wetlands, would undoubtedly read this book with different eyes and strongly disagree with this preliminary assessment; wetlands conservation is a major topic of this book.

The preface brings a personal touch to Harrington's introduction to the world of shorebirds when, a teenager in the early 1950s, he first "discovers" Golden Plovers along the Sakonnet River in Rhode Island. And his fascination with shorebirds never diminished. The first time I picked up this book, I was anxious to learn much about a fascinating species about which much had been documented by the author in the scientific literature. I looked forward to reading about all of Harrington's work on the Red Knot summarized in a single book. But I was disappointed: the introduction is about wetlands and their importance to shorebirds in general; the Red Knot is not mentioned until the fifth page of the introduction. I found that the book went to great lengths to deal with environmental and conservation issues, some of which have long been dealt with (e.g., Fundy tidal power, see below), and not enough, in my opinion, about the interesting dynamics and biology of a fascinating migrant.

Overall, Chapters 1 to 3 deal with the Red Knot's northward migration; those three chapters are subdivided by region and time of year (e.g., from the wintering grounds in October through February (Chapter 1) to the shores of Delaware Bay in May and June (Chapter 3)). The months of June through August describe the breeding season in the arctic (Chapter 4) while Chapter 5 returns the reader back to the wintering grounds (August through October). The final chapter (Into Our Future) concentrates on the potential threats to shorebirds and the many conservation programs in place to protect their habitats.

The species we know as Red Knot is not fully introduced to the reader until page 31 in the chapter entitled "October through February." In this reader's humble opinion, the first paragraph of page 31 should really be the first paragraph of the book. It is a tedious introduction to the species and one which probably works better on film than in book form. But Harrington's thought-provoking description of knots in flight followed by Twichell's photo on page 42 is a most effective technique in describing/showing the great beauty of, and mystery in, flying shorebirds.

Harrington indicates "that we have little idea" how the Red Knots manage the flight from Lagoa de Peixe in Argentina to Delaware Bay in New Jersey/Delaware. However, the "possible" explanations given by Harrington are fascinating enough to turn a large number of the readers into shorebird biologists to find the answers. But the first descriptions of the trans-Atlantic migration of knots are placed in a footnote (Note 7, see third paragraph) and will likely be missed by many readers. Similarly, the mention of picric-dyed knots (of which much has been published by Harrington), is simply made in the legend to a photo of dyed knots on page 106; it is especially relevent (and most interesting) information and really should have been expanded in the text.

Chapter 6 is essentially the environmental lecture. It makes reference to (1) the Exxon Valdez, (2) hydroelectric dams in James Bay and (3) Fundy tidal power. The two latter issues were problems in Canada which were heatedly discussed by the scientific community a decade and a half ago. No details of these debates are given. This chapter goes to some length to discuss shorebird conservation programs in Delaware Bay; it reads like a dull but factual government report. A similar lengthy discussion about Jamaica Bay goes into considerable detail about parking space and the like and, in my opinion, is examined in more detail than is really necessary in this book. This chapter also reads like a lecture on the philosophy of conservation in the modern world; all very commendable, but what has it to do with the flight of the Red Knot?

I have long admired Harrington's scientific work and dedication to the task, so my disappointment with this book is mainly due to my high expectations. Consequently, I found it most unfortunate that Harrington's scientific papers are not listed anywhere in this book. The main lesson here is that a nature film is not easily transformed into a book. I unfortunately never saw the film ("Mystery of the Animal Pathfinders" by NOVA) but my impression is that the reverse scenario is probably more successful. But I must stress here that the great beauty of this bird is done considerable justice by the remarkable photography of Dave C. Twichell.

Overall, these two publications provide considerable valuable information on the migratory movements of a species on a worldwide basis. But I can only conclude that Piersma and Davidson's collection of papers (including a paper co-authored by Harrington) have considerably more scientific merit than the adaptation of a nature film can convey.—PETER HICKLIN.

SPARROWS AND BUNTINGS—A GUIDE TO THE SPARROWS AND BUNTINGS OF NORTH AMERICA AND THE WORLD. By Clive Byers, Jon Curson, and Urban Olsson. Houghton Mifflin, Boston, Massachusetts. 1995. 334 pp., 39 color plates with captions, 110 range maps, $40.00 (cloth)—This is the eighth volume to appear in Houghton Mifflin's "Helm Identification Series." This volume covers the buntings and sparrows (subfamily Emberizinae) of the

Holarctic region, not "the world," as the title suggests, since the authors clearly state in their introduction that ". . . to include all the South American species would really be beyond the scope of the book . . ." Small oversights such as this aside, this is a very good guide to field identification for a challenging group of species. Brief introductory chapters on "Taxonomy and Relationships," "Breeding Biology," "Escaped Cagebirds," and "Hybrids" add interest to the book. The chapter, "Taxonomy and Relationships," is especially useful. One hundred ten species are covered, with range maps for each species. The tendency of the book is to be rather inclusive of species, rather than exclusive, with some forms of uncertain taxonomic status, such as "Timberline" Sparrow (*Spizella* (*breweri*) *taverneri*) included in the text and treated as distinct species.

In general, the color plates are good; however, in my review copy the color saturation from plate to plate was quite variable, with some plates noticeably brighter than others. Each plate undertakes to depict multiple species, along with distinctive plumages for juveniles and adult males and females. This leads to some very "busy" color plates in some instances (e.g., Plate 18: American Longspurs and Plate 36: Rufous-sided/Collared Towhee Complex) and the arrangement of species on the page can be confusing at times (e.g., Plate 33: *Aimophila* Sparrows).

Each species account includes information related to identification (mostly field marks), detailed description (including plumage differences among the sexes and juvenile and adult birds), aging and sexing guidelines, measurements, geographical variation, voice, habits, status and habitat, distribution, and references. The emphasis of the species accounts is upon identification, with relatively less information on other aspects of a species' biology, and the references cited are highly variable, both in quantity and quality. Information about status is usually not very useful, with general terms, like "common," "uncommon," or "fairly common" used frequently without any interpretation of their meaning.

In addition to the color illustrations of birds, I also found the extensive set of range maps provided with the book of special interest. Unfortunately, it has become popular in recent years to use guesses at the areas of species ranges as components of various, arbitrary, conservation ranking schemes. Like most range maps produced in field guides, the maps in this book are reproduced at unspecified scales, coordinate systems, and projections, making them illustrations, not maps, and unsuitable for estimation of any actual land areas associated with the range of a species. The cartographically challenged, therefore, should be careful in their use of these maps for purposes other than illustrations, since they are not "maps" in a technical sense and not intended for technical uses.

I found this book to be a good overview of a diverse and challenging group of species. I recommend it to anyone with a specific interest in field identification of sparrows and buntings or a general interest in worldwide distributions and general ecology of those groups.—CHARLES R. SMITH.

CHICKADEES, TITS, NUTHATCHES AND TREECREEPERS. By Simon Harrap and David Quinn. Princeton Univ. Press, 41 Williams St., Princeton. New Jersey 08540. 1996: 464 pp., 36 color plates, 110 color maps. $49.50.—The Great Tit (*Parus major*) may be the most intensively studied bird in the world, while the Black-capped Chickadee (*P. atricapillus*) is certainly one of the most familiar birds in North America. These two species are the stars of the latest in the series of monographs devoted to single or closely related bird families. Other familiar birds of western Europe and North America and a long list of little known Asiatic species are included. Following the taxonomy of Sibley and Monroe, the book treats the Sittidae (25 species), Certhiidae, including *Salpornis* (7 species), Parinae (57 species),

Remizinae, including *Auriparus*, (13 species), and Aegithalidae, including *Psaltriparus* (10 species).

Even though two publishers are marketing the American versions of these originally British books they both follow a standard format. (By a complicated set of events two British companies are also involved.) A short introduction is followed by a section of color plates together with range maps. A third section gives a detailed discussion of each species under the topics: Identification, Sex/Age, Voice, Distribution and Movements, Habitat, Population, Habits, Breeding Biology, Description, Moult, Geographical Variation, Relationship, and References. The species accounts vary in length from a page and a half to 14 pages for the Great Tit and 10 for the Black-capped Chicakadee. For the well-known species these accounts are much fuller and offer more information than has been the case in other books in the series. The text, indeed, makes a very useful summary of the biology of the species. An authority of a given species may find the accounts lacking something, but they appear to be accurate summaries of the available literature. Scattered through the species accounts are numerous black-and-white figures, sound spectrograms of vocalizations, maps detailing distribution, tail or wing patterns, or other identification characters.

The colored figures by David Quinn are quite good. Quinn has pretty well avoided the big-headed appearance that have characterized some of the drawings in this series. However, a few of his birds could not possibly stand upright on the legs and leg attachment he has given them. Several plumages are figured for each species with 20 for the Great Tit. Of course all these tits look alike, as witness plate 16 with 14 figures of three species with only very subtle differences.

The range maps are small but reasonably accurate. A few show a very limited area on a blown-up section of a map of central Asia. Without labels the normal reader will have difficulty in placing this range.

Most *Wilson Bulletin* readers will use the treatment of the Black-capped and Carolina (*P. carolinensis*) chickadees as a test of this book. I can report that it passes this test with a good score. The British author has certainly done his homework on this matter. The details of the plumage and vocalization differences are carefully and completely outlined. These two species do however, overlap in parts of the Appalachians to an extent greater than indicated.

While the book is well done and full of interesting information, I am left with a wonder as to what audience it is intended. Some of the introduction is at the very elementary level. On the other hand the detailed description of all the described subspecies (33 for *P. major*) would appear useful only to a taxonomist. The detailed feather by feather descriptions would be of use only for banders or museum curators identifying specimens. As other reviewers of books in this series have noted no one is going to carry these books into the field to identify birds encountered in a new region. Indeed the traveling birder will not even take these books along for consultation. He will take a field guide for the region he is visiting. It would appear then that the authors and editors of this series want to produce a series of all-purpose books, sort of "Handbuch" on the inexpensive side. If so they have accomplished this volume is done in a first rate manner.—GEORGE A. HALL.

THE DOUBLE-CRESTED CORMORANT: BIOLOGY, CONSERVATION, AND MANAGEMENT. Edited by David N. Nettleship and David C. Duffy, Colonial Waterbirds 18 (Special Publication 1):1–256, $30 postpaid (paper).—The Double-crested Cormorant (*Phalacrocorax auritus*) is arguably the most volatile avian species of this century. It has gone from locally extirpated human food item (early 1800s), to locally abundant pest species

(1950s), to endangered status in much of its range (1970s) and to an exploding continental population carrying major implications for aquaculture and disease transmission (1990s). This issue of "*Colonial Waterbirds*" is devoted entirely to the proceedings of a symposium on Double-crested Cormorants held in Oxford, Mississippi, in 1992. The proceedings contain 29 scientific papers, involving 67 authors, organized into four major sections. In "The Bird and the Problem," three papers document the history of the North American population, the potential interactions of cormorants with rapidly growing U.S. and Canadian aquaculture industries, and the sociology of human perceptions of cormorants as competitors with humans for fish.

The second section, "Regional Distribution, Status and Conflicts," gives a wealth of specific information about the various regional populations and how humans have dealt with the problem of cormorant depredations on fisheries and aquaculture. This section is clearly the largest (19 papers) and most varied, with contributions on population dynamics, food habits, energetic predation models, techniques for mitigating depredations, conservation on the Pacific coast, breeding success, management histories, and effects of toxic chemicals. This is clearly the meat and potatoes of the volume; it documents the actual state of knowledge about this species, and provides data-rich reference material such as nest counts for specific colonies and regions, contaminant levels, and regional differences in morphometrics.

Part three, "Management Responsibility," is comprised of three papers representing the self-percieved management responsibilities of the U.S. Fish and Wildlife Service, the U.S. Department of Agriculture, and Environment Canada. Although this is the least scientific section, it does highlight how fractured management responsibility is across the U.S. Federal Government and among the Provinces of Canada.

The last section, "Conclusions and Recommendations," is comprised of two papers, one dealing with the future needs of research, and one summarizing the symposium as a whole. This section is particularly valuable since both contributions are hard-hitting, identifying major areas of information that are lacking, and suggesting novel approaches, such as that the cost of research to identify management options might not actually be justified by the cost of depredations to the industry.

The cormorant story is remarkable from many viewpoints. Cormorants have displayed extreme volatility in population size and growth rate, have responded rapidly to the rise and fall of contaminant levels, are a classical example of public perception of pest status repeatedly overriding scientific evidence to the contrary, and have demonstrated just how rapidly a species can shift from a species of local conservation priority to one of national industrial interest. This is a history that should be required reading for ornithogists, wildlife managers and animal ecologists.

This volume is most certainly not for the amateur ornithologist, since it is presented in symposium style, and the papers written in scientific, heavily referenced format. It is professionally edited and printed to the standards of scientific journals. As a guide to the current knowledge of the species, this volume does excellent service, being by far the most up to date body of literature on Double-crested Cormorants, and is the sole document to address comprehensively the growing conflict between cormorants and aquaculture. The volume is valuable both because it is comprehensive, and because the richness of its data will allow it to stand as a valuable reference document for many years to come. I recommend this book highly for professional ornithologists, wildlife managers, aquaculturists, agencies involved in management of aquaculture and fisheries industries, and especially, libraries.—PETER C. FREDERICK.

THE PENGUINS. By Tony D. Williams, illus. by J. N. Davies and John Busby. Oxford Univ. Press, Oxford. 1995: 295 pp., 8 color plates, 17 range maps, 112 numbered text figs., 54 tables. $65. (Hardbound).—This book is an authoritative account of the world's 17 species of penguins. The only remotely comparable compilation is contained in "Handbook of Australian, New Zealand and Antarctic Birds" (Marchant, S. and P. J. Higgins, eds. 1990, Oxford Univ. Press, Melbourne), which, like the present work, uses color paintings by J. N. Davies to illustrate all species. There is considerable overlap between the species accounts in the Marchant and Higgins' "HANZAB," but that book does not cover penguin species from South Africa, South America, or the Galapagos Islands and is five years less up-to-date than Williams in literature citations.

The present volume has two major subdivisions. The first of these includes eight introductory chapters on various aspects of penguin biology and the second contains the seventeen detailed species accounts.

The introductory chapters are comprehensive and up-to-date. They cover evolutionary origins, breeding biology, population dynamics, behavior, foraging ecology, physiology, and conservation. Of especial interest to me, both because of my personal interests and the extent of scientific advance presented, was the chapter on "foraging ecology" written by R. P. Wilson. This chapter summarizes recent information obtained from a variety of recently developed electronic recording devices implanted in penguins - in combination, these instruments permit the tracking of individual penguins on their foraging trips and recording when (and *where*, from satellite-tracked transmitter) on these trips they catch prey. Also exceptionally rich in new information was the chapter on "population dynamics"—here the advances derive from the several long-term studies of penguins that have recently yielded published results. Williams has left most literature references out of the text in the name of readability; this is at times annoying, as many statements, clearly based on single studies, are presented as if universally true. For example, on page 34 it is stated, without reference, that "In Adelie Penguins breeding success increases in birds up to 7 years of age, averaging 0.3 chicks per pair in 3 year-old-birds." There are many such examples. In his well-written and useful chapter on "population structure and dynamics," Williams alludes to the intertwined problems of estimating dispersal and survival in penguins. In many past studies, birds that disperse are implicitly assumed to have died, resulting in exaggerated estimates of philopatry and underestimates of dispersal distances. This is an issue with important conservation implications that I think deserves more attention, and the information in this chapter is a good start.

The species accounts are thorough and incorporate very recent information. They are more than just a good update; there is qualitatively new information being included. For example, data on "Age of First Breeding" are included for nine out of the seventeen species treated. Since these data require a minimum of 5–10 years of continuous study to collect, their inclusion attests to the seriousness of effort devoted to the study of penguins in recent years.

Penguins, the quintessential polar animals, have much to offer even the most jaded biologist. From this book, one will learn of first-laid "runt" eggs of the *Eudyptes* penguins that never hatch, squandering of reproduction by 20% of individuals in a Little Penguin (*Eudyptula minor*) colony, the disappearance to locations unknown by many species of penguins in winter, and of course the extraordinary vigil of Emperor Penguins (*Aptenodytes forsteri*) and their chicks through the intense cold and isolation of the Antarctic winter.

In summary, this is an excellent book that all seabird biologists and zoological libraries will want to own. Animal ecologists will at least want to read the introductory chapters, and it is hard to imagine anyone whose interest would fail to be piqued by the lives and antics of this remarkable group of birds.—RICHARD R. VEIT.

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Dr. Robert C. Beason will serve as Editor of *The Wilson Bulletin* beginning with Volume 110. All manuscripts submitted for publication in the *Bulletin* should be sent to him at this address:

Dr. Robert C. Beason
Biology Department
State University of New York
1 College Circle
Geneseo, NY 14454

email: beason@uno.cc.geneseo.edu
(or) wilsonbull@uno.cc.geneseo.edu

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Editor Charles R. Blem
Department of Biology
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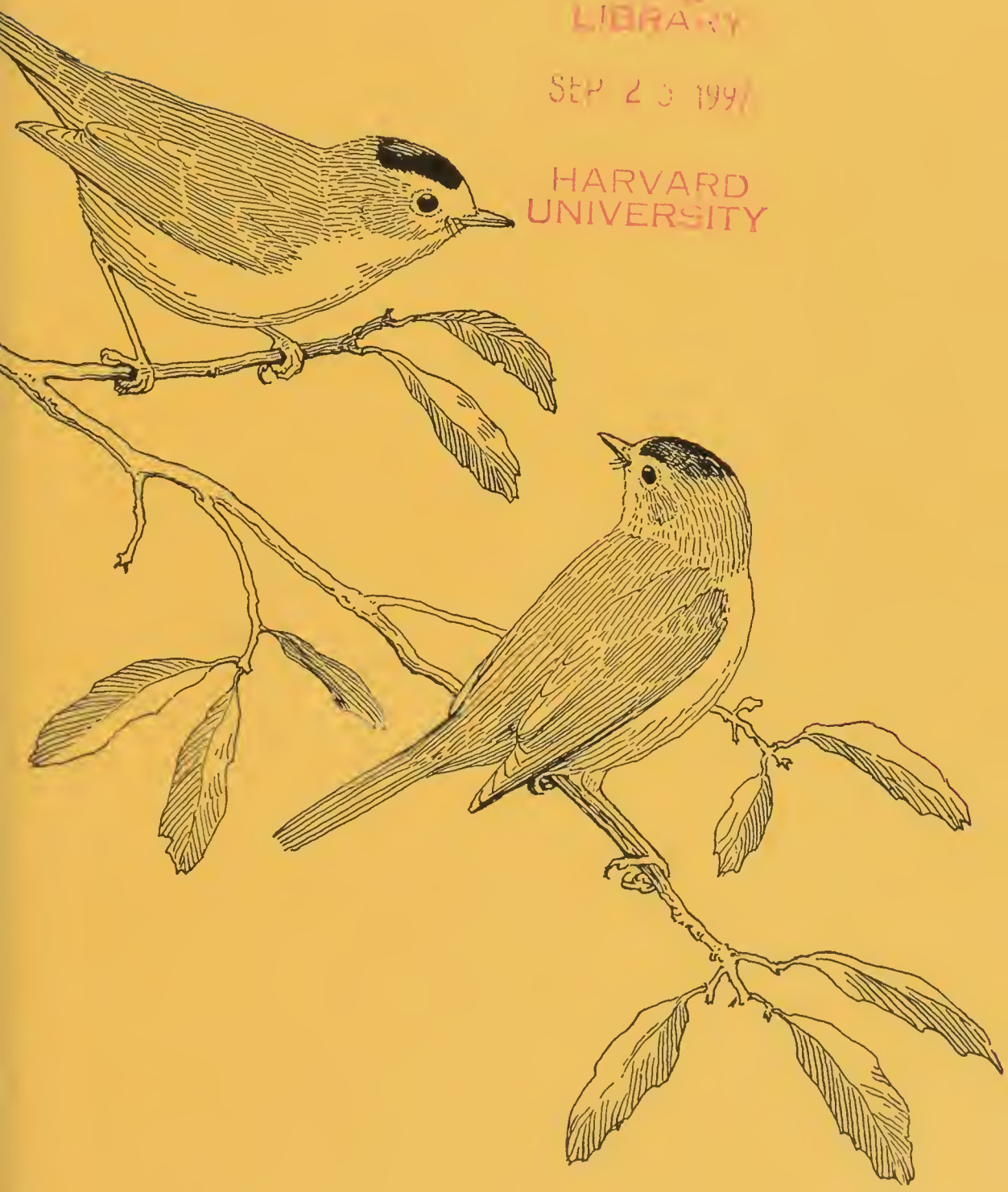

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Frontispiece. The Velvet Asity (*Philepitta castanea*). Alternate, definitive plumage male (upper left) performing the Hanging Gape Display; basic definitive plumage male (middle right); and female (lower left). Inflorescence in upper right is *Bakerella clavata* (Loranthaceae).

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LEK BEHAVIOR AND NATURAL HISTORY OF THE VELVET ASITY (*PHILEPITTA CASTANEA*: EURYLAIMIDAE)

RICHARD O. PRUM[1] AND VOLOLONTIANA R. RAZAFINDRATSITA[2]

ABSTRACT.—Observations of territoriality, vocalizations, display behavior, and nesting of the Velvet Asity (*Philepitta castanea*: Eurylaimidae: Philepittinae) indicate that this species is polygynous. Males defend nonresource-based, display territories that are distributed in dispersed leks. Male display repertoires include six elaborate secondary sexual display elements which are performed in both intrasexual and intersexual contexts. Pairs of female-plumage birds construct the nest outside of male territories, and females perform post-fledging parental care. Occasional observations of adult males in association with female-plumaged birds at the nest indicate potential plasticity in breeding behavior within the species. The evolution of the breeding system, display behavior, plumage, delayed male plumage maturation, and molt of the asities is discussed in a phylogenetic context. Two displays of *P. castanea* originally evolved in the common ancestor of the asities. The distinctive appearance of *P. castanea* in the breeding season is a worn basic plumage which has evolved by acquisition of a sexually dichromatic basic plumage and the loss of the prealternate molt. Delayed plumage maturation originally evolved in the common ancestor of the genus *Philepitta*. An additional, distinctive, predefinitive plumage stage-class has evolved in Schlegel's Asity (*P. schlegeli*).
Received 27 Feb. 1996, accepted 7 April 1997.

The asities are a monophyletic group including two distinct genera—*Philepitta* and *Neodrepanis*—that are endemic to Madagascar. *Philepitta* includes two species of medium-sized (~40 g), forest birds with diets that consist of fruit and nectar. *Neodrepanis* includes two species of sunbird asities—very small (6–8 g; Goodman and Putnam, 1996), forest nectarivores with long decurved bills that are remarkably

[1] Natural History Museum, and Dept. of Systematics and Ecology, Univ. of Kansas, Lawrence, Kansas 66045-2454.

[2] Ranomafana Natural Park Project, and Université d'Antananarivo, B.P. Box 3715, Antananarivo (101), Madagascar.

convergent with many sunbirds (Nectariniidae), hummingbirds (Trochilidae), and Hawaiian honeycreepers (Drepanidae). Traditionally treated as a separate, isolated family of suboscines (Amadon 1951, 1979; Raikow 1987), asities have long been recognized as a striking example of adaptive radiation (Salomonsen 1965). Recent phylogenetic analysis of the group has documented that the asities are a Malagasy lineage of the Old World tropical broadbills (Eurylaimidae; Prum 1993). In the phylogenetic context of the broadbills, the adaptive radiation of the asities is even more extreme given that *Neodrepanis* species could be appropriately called "sunbird-broadbills."

The Velvet Asity (*Philepitta castanea*) is an understory forest frugivore that is distributed throughout the rain forests of eastern and northern Madagascar (Langrand 1990). Recent field studies have documented that the diet of Velvet Asity is composed of a wide variety of fruit species and nectar from various plants (Goodman and Putnam, 1996; V. R. Razafindratsita and S. Zack, unpubl. data). Most other aspects of the natural history of *P. castanea* remain poorly known.

P. castanea shares a number of striking ecological and morphological similarities with several groups of well known, polygynous tropical passerines. Like many manakins (Pipridae), cotingas (Cotingidae), birds of paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae), *P. castanea* is primarily frugivorous, is highly sexually dimorphic in plumage, has elaborate secondary sexual characters (e.g., brightly colored, fleshy caruncles), and delayed male plumage maturation. The presence of this unusual and distinctive combination of characters first lead us to investigate the nature of the breeding system of this species. Our observations indicate that *Philepitta castanea,* like many other species of frugivorous tropical passerines, is polygynous and breeds in a dispersed lek system. These preliminary observations document that the behavioral diversity of the Old World suboscines is even broader than currently realized.

STUDY AREA AND METHODS

The observations were made in an area of secondary humid tropical forest in Ranomafana National Park, Ranomafana, Ifanadiana, Madagascar (21°16′S 47°28′E). The study site included a roughly 10 km^2 area near the park entrance. Specific localities of territories and nests found in the study area are referred to here by the trail name and the meter number nearest the site (e.g., A-1100—meter 1100 of trail A).

Initial observations of territorial males were made during the 1993–94 breeding season by V. R. Razafindratsita between 24 Nov.–15 Dec. 1993 and 23 Jan.–1 Feb. 1994, and by R. O. Prum on 22–25 January 1994. The second field season was from 2–29 November 1994. Twenty-four Velvet Asities were banded with distinct color combinations in the study area between 1991–1993 by S. Zack and colleagues. An additional seven individuals were

banded by the authors in November 1994. Three of these latter birds were subsequently observed as territorial males.

All observations were made with binoculars and without blinds between 5 and 20 m from the birds. Tape recordings of vocalizations were made using a Sony TCM-5000 with a Sennheiser ME-80 microphone. Spectrograms were prepared using Canary 1.2 (Charif et al. 1995). Video tape recordings of Velvet Asities were made using a Canon L2 high-8 mm camera. Data for ethograms of focal territorial males was taken using 5-min observation periods. During each 5-min observation period, we recorded whether the male was present in, exited, or entered the territory; the position and height of its perch; changes in perch; vocalizations or displays; intraspecific and interspecific interactions; foraging events; regurgitation; and preening. A total of 40 h of observations of eight territorial males was completed.

Information on plumage and morphology was gathered from observation of museum skins in the collections of the American Museum of Natural History (AMNH), New York, the Field Museum of Natural History (FMNH), Chicago, and the Muséum National d'Histoire Naturelle (PM), Paris.

RESULTS

Plumage and morphology.—The plumage of female *P. castanea* is dull green above with wide green and gray longitudinal stripes below (see Frontispiece). The legs are grey, the bill black, and the iris dark brown. The definitive plumage of adult male *P. castanea* changes seasonally. Adult males go through a complete prebasic body molt sometime between February and May (earliest in northern Madagascar). The fresh, definitive basic plumage male (or adult nonbreeding aspect) is black on the face, throat, and flight feathers, and black with olive green feather edgings over the rest of the body (See Frontispiece). The green feather edgings wear off and ultimately produce a distinctive, black appearance during the breeding season (which is refered to here as the breeding aspect of the definitive basic plumage). The definitive male breeding aspect is velvety black with a bright yellow spot on the upper marginal alular wing coverts (See Frontispiece). These yellow "wrist" feathers are usually concealed when an adult male is perched. There is no prealternate molt. Thus, the definitive male breeding aspect is a worn basic plumage, not a distinct plumage produced by a distinct molt. During the transitional period from nonbreeding to breeding aspect, males are individually identifiable by the distinctive patterns of wear of the green feather edgings. Little is known about the molt of females, predefinitive males, or flight feather molt in either sex. There is no sexual dimorphism in size (Goodman and Andrianarimisa 1995).

Definitive breeding aspect males also have a pair of brilliant fleshy supraorbital caruncles (Prum et al. 1994). The caruncle is mostly bright, vivid green with a central horizontal sky blue stripe above the eye. At rest, the caruncle is a flaccid and wrinkled flap of unfeathered

skin above the eye (Fig. 5). The rostral portion of the caruncle is a flat, rounded lobe that lies over the culmen. The caudal portion of the caruncle is a narrow, wrinkled strip that lies above the eye and curves ventrally below and behind the eye. The horizontal blue stripe is concealed within a prominent horizontal wrinkle or fold in the center of the caruncle above the eye. The caruncle is covered with tiny cone-shaped, keratinized papillae that include macrofibrils of collagen that produce the structural color (Prum et al. 1994). At rest, the caruncles vary in size and shape within and among males. Some males are individually distinguishable by particular features of their caruncles, particularly the wrinkled dorsal margin and the extent of curvature below and behind the eye. Males can immediately erect the caruncles into two straight planes above the eyes (Fig. 2). When the caruncle is erect, the rostral and caudal portions of the caruncle straighten, and extend upward, exposing the bright blue central stripe. The erection of the caruncles is a prominent feature of the erect posture and wing-flap display performed by territorial males (see below). The shape and position of the caruncles are under immediate muscular control. Video tape recordings of males document that they can move the caruncle instantaneously. Histological sections of the caruncle also show prominent striated muscle tissue in the caruncle that presumably controls its shape (Prum et al. 1994: fig. 2, lower left).

The caruncles of males are absent in nonbreeding, basic plumage males. They apparently develop annually before the breeding season (between June and November, depending on latitude). Nothing is known about the mechanism of development of the caruncles.

Predefinitive males have enlarged gonads, essentially female-like plumage and lack developed caruncles (Rand 1936; Benson 1976:367–369; S. M. Goodman, pers. comm.). At least some, and perhaps all, predefinitive males can be distinguished from females in the hand by a whitish, featherless patch of skin above the eyes, which is the precursor of the definitive caruncle of adult males (Prum et al. 1994; R. O. Prum, pers. obs.; FMNH 345697). Predefinitive males also vocalize and perform rudimentary displays (see below). Nothing is known about the amount of time male *P. castanea* spend in predefinitive plumage before they acquire definitive male plumage and caruncles.

Male territoriality.—Observations were made of eight territorial, adult male *castanea* in two subsequent breeding seasons (Table 1). Male territories are approximately 10–20 m in diameter. Most territories identified were adjacent to another male territory, with territory centers less than 50 m apart (ER-0 and ER-35; A-1100 and A-1110; π-25, π-75, and π-125). In all of these cases, males in adjacent territories were within

TABLE 1

TERRITORIAL ATTENDENCE BY MALE VELVET ASITY (*PHILEPITTA CASTANEA*) IN RANONOMAFANA NATIONAL PARK, MADAGASCAR

		1993–1994			1994–1995
Individual	Locality	Dec	Jan	Feb	Nov
UB#1-GRWW[a]	A-1100	*	*	*	*
UB#2	A-1110	*	*	*	
UB#3	ER-0	*			*
WYRR[a]	ER-35				*
UB#4-GWOO[a]	E-10	*	*	*	*
UB#5	π-25			*	
UB#6	π-75			*	
UB#-7	π-125			*	

* Territorial, adult male was cited at this locality during that month.
[a] Banded during November 1994.

auditory range of one another. Only a single male (GWOO, E-10) was out of immediate hearing range of other known territorial males; he was 125 m from the closest other male. Three males banded in early November 1994 were subsequently observed defending territories later that month. Two of these three males occupied the same territories and used the same vocalization perches as unbanded males in January 1994, during the previous breeding season. An unbanded male (UB#3) was also observed in the same territory in two consecutive breeding seasons. This male was individually identifiable by plumage and caruncle shape during ten observation days in late November 1994. Males were not observed defending territories until they had completed a majority of the transition from the nonbreeding basic asect to the worn, breeding aspect of the basic plumage (i.e. were mostly black). Additional observations are required to confirm this conclusion. Predefinitive males were not observed defending territories.

Males advertise and defend territories by perching on a horizontal branch or liana between 1–5 m above the ground (x = 2.5 m, N = 218) and calling (see below). Males were observed using more than 20 different vocalization perches within a territory, but a few specific perches were usually preferred. Male territorial attendance varied with season. From December 1993 through early February 1994, males were present on territory for 63–92% of 5-minute observation periods between 05:30 and 16:00. In early November 1994, males were not territorial. Between 20–29 November 1994, apparently at the beginning of this breeding season, males were present on territory between 40–70% of 5-minute periods

FIG. 1. Spectrograms of vocalizations of the Velvet Asity *Philepitta castanea* at Ranomafana National Park, Madagascar. (A) The advertisement call (*weee-dooo*); and (B) the long call (*weet . . . weet . . .*).

between 05:30 and 8:30. Later in the day, territorial attendance dropped off completely.

Males frequently left their territories for short periods to forage or interact with other birds (N = 99; 28% of observation periods with male in attendance). Limited food resources were located within male territories and males occasionally did forage within their territories, but males most frequently left the territory to forage elsewhere.

At Ranomafana, female *castanea* build nests exclusively in a single species of tree (*Tambourissa obevata,* Monimiaceae; see Nesting below). Five male territories that were carefully surveyed did not include a single individual of this common tree species (A-1100, A-1110, ER-0, E-10, π-25).

Vocalizations and mechanical sounds.—Males give a high, thin, squeaky advertisement vocalization that is a pair or short series of *weee-dooo* notes, with a conspicuous emphasis on the first syllable. Each *weee-dooo* phrase is characterized by an initial note that rises from ~5.5 to 6.3 kHz over 100 ms, a 50 ms pause, and a final note that descends from ~5.4 to 4.8 kHz over 150 to 190 ms (Fig. 1A). This vocalization is inconspicuous, low in amplitude, and can be difficult to detect at more than 20 m away.

During male-male interactions (see below), males give a long call, which is an energetic, nearly continuous series of call notes similar to the initial syllable of the advertisement call—*weet . . . weet . . . weet . . . weet.* Each *weet* note rises ~1–3 kHz over 80 ms from between 5.5–6.3 kHz to 7.4–8.2 kHz, and are separated from one another by 0.75 to 1.5 s (Fig. 1B). Series of long calls can be given continuously for minutes.

A third rare vocalization, a high thin *seeeeee* call, was heard on several

TABLE 2

FREQUENCY OF VOCALIZATION AND DISPLAY ELEMENTS BY MALE VELVET ASITY (*PHILEPITTA CASTANEA*) IN RANONOMAFANA NATIONAL PARK, MADAGASCAR

	N	Frequency over all observation periods[a]	Frequency with male in attendance[a]
Territorial Attendance	335	65%[c]	—
Advertisement Call	495	10.9	16.7
Long Call Bouts	36	0.80	1.23
Wing Flap Pump	75	1.70	2.50
Open-Gape Display	15	0.33	0.50
Hanging Gape Display	5	0.11	0.17
Perch-Somersault Display	2	0.04	0.62

[a] Mean observations per hour over all 542 5-min. observation periods.
[b] Mean observations per hour over the 355 5-min. observation periods with the male in attendance.
[c] % of the 542 5-min. observation periods with male in attendance.

instances during interactions between territorial males. This vocalization was not recorded.

Presumed predefinitive males with female-like plumage were observed and recorded giving both the advertisement and long calls during visits to established territories and while following foraging females.

Adult males produce a notable whirring sound during flight that is presumably produced by the wings. This sound was heard during both display and foraging, and did not appear to be modulated or controlled by the male. Female-plumage birds were not observed making this wing noise, but this may be a result of limited observations at close distances. It is not known whether this wing sound serves as a sexually dimorphic acoustic advertisement, or whether their is sexual dimorphism in the shape of the remiges.

Territorial male *castanea* vocalize relatively infrequently (Table 2). The *weee-dooo* advertisement call was given an average of 10.9 times per observation hour (16.7 times per hour during the five-minute observation periods when the male was on territory). Long call bouts were observed 36 times at an average frequency of 0.8 bouts per observation hour. Vocal activity is greatest in the morning between 06:00 and 10:00, but precise measures of daily temporal variation are skewed by the greater number of morning observation periods.

Display elements.—Six complex male display elements were observed: (1) the erect posture, (2) the wing-flap pump display, (3) the horizontal posture, (4) the open gape display, (5) the hanging gape display, and (6) the perch-somersault display.

In the erect posture, the male assumes an erect, "rooster-like" pos-

FIG. 2. The erect posture of the Velvet Asity *Philepitta castanea.*

ture with its neck and body elongated and leaning forward over the perch, and erecting the brilliant green and blue caruncles (Fig. 2). When erect, the caruncles are raised into two planes running from the base of the beak to above and behind the eye, resembling two sides of a tricornered hat, and exposing the light blue horizontal stripe above the eye. The erect posture is strikingly different from the typical inert, pear-shaped appearance of perched *P. castanea* when perched. (An accurate account of the frequency of the erect posture was not recorded because this display was not identified as a distinct element until late in the observations).

Performances by two different males of the wing-flap pump display were observed well. One male maintained the erect posture for 1–2 s, and suddenly leaned forward and horizontal over the perch. The male then briefly pumped up and forward, pointing its beak, fully extending its neck, raising up on its long tarsi, and returning back to erect posture on the perch. Then after a short pause, the male performed a second vertical pump and opened and closed both its wings simultaneously

FIG. 3. The wing-flap pump display of the Velvet Asity *Philepitta castanea.*

(Fig. 3). At this moment, the body is at its most erect position, and the broad black wings were held open vertically at the sides and parallel to the body (Fig. 3). The yellow alular covert wing spots were also prominently flashed against this dark, bat-like profile. In a single video tape recording of this male displaying, the first and second pumps were 0.23 and 0.26 s long, respectively, with a single 0.1 s pause in between them. In the wing-flap pump display of a second male, the two pumping movements were immediately followed by a series of two to five asynchronous, single wing flaps that were performed without pumping movements. The order in which each wing was flapped appeared random. Each male always performed the display in the same fashion. The display is performed silently. A total of seventy-five performances of the wing-flap pump by five different males were observed, for a frequency of 1.70 displays per observation hour (Table 2). Males were observed assuming the erect posture without proceeding to the wing-flap or pumping movements.

In the horizontal posture, the male assumes a sleek horizontal position on the perch with the neck elongated (Fig. 4). Typically, the horizontal posture is assumed after a male has heard the call of another neighboring male. The male then peers intently for a brief period and then flicks his wings once or twice before leaving the perch. (An accurate account of

FIG. 4. The horizontal posture of the Velvet Asity *Philepitta castanea.*

the frequency for the horizontal posture was not recorded because this display element was not identified until late in the observations).

In the open gape display (N = 15), a male perches with its head pulled in, and its mouth open wide held up at a slight angle, prominently exposing the bright yellow gape (Fig. 5). While perched in this posture, the male may open its mouth silently or give an extended and energetic series of long calls. Frequently, the male flies from perch to perch, giving con-

FIG. 5. The open gape display of the Velvet Asity *Philepitta castanea.*

FIG. 6. The hanging gape display of the Velvet Asity *Philepitta castanea.*

tinuous long calls, and assuming the open gape posture on each perch. The caruncles are not raised during the open gape display. The open gape display was infrequently observed (Table 2).

On several occasions (N = 5), males performed a fifth elaborate display movement. In the hanging gape display, a male in the gape posture suddenly throws itself forward and downward with an awkward flap of the wings and hangs from the perch (Fig. 6). The hanging male faces forward with its head held horizontal, its wings closed, its tail nearly vertical and above the perch, and its gape open. After 0.5 to several seconds, the male flies from the perch. Sometimes, the male continues giving long calls throughout the display. The sudden initiation of the hanging gape display looks as if the male were about to fly from the perch but accidentally tripped over its long toes while leaving.

A distinct perch-somersault display was observed twice (N = 2) being performed by two different males. During this display, the male appeared to initiate a hanging gape display, but instead of hanging, it completely rotated around the perch to resume a normal open gape display posture.

Presumed predefinitive males in female-like plumage were observed performing the erect posture, the wing-flap pump display, and the open gape display.

Intraspecific interactions.—Territorial males frequently interact with

other individuals including adult males, and presumed predefinitive males and females. Interactions among adult males usually began as bouts of countersinging between territorial neighbors (N = 29). After a few calls each, countersinging males frequently left their perches, and approached each other along their mutual territorial boundaries. Neighboring adult males were never observed intruding directly on a male's territory. Interactions with predefinitive males (N = 7) were similar but predefinitives occasionally enter a male's territory directly. Predefinitive males were identified by their female-like plumage, advertisement vocalizations, postures or displays, and frequent aggressive perch changes.

The open gape and hanging bow displays were most frequently performed during competitive male-male interactions. Two males commonly perch <5 m apart at the boundary of their territories, vocalized energetically, chased one another, and performed repeated open gape displays and occasional hanging gape displays.

On most occasions, the erect posture and the wing-flap pump display were performed in response to a second, unobserved bird. On five occasions, visits to male territories by presumed females were observed. These female-plumage individuals did not call, posture, or act aggressively toward the resident males, as did presumed predefinitive males. After excited advertisement calling, territorial males became silent and performed the erect posture and wing-flap pump displays repeatedly until the female exited the territory. Interactions between territorial males and presumed females were frequently disrupted by the distracting activity of neighboring males. On several occasions, two adult males pursued a presumed female off their territories with repeated calls and displays. No copulations were observed.

In general, the horizontal, open gape, and hanging gape displays appear to serve an intrasexual, competitive function, whereas the erect posture and the wing-flap pump display serve an intersexual function. On some occasions males performed the erect posture or the wing-flap pump display during interactions with other males, but in several of these cases it appeared that another unseen individual, perhaps female, was present.

Interspecific interactions.—Territorial male Velvet Asity occasionally responded to intrusions of other species on the territory. Several times, wing-flap pump displays were performed by males in response to a bird of another species—e.g., Blue Coua (*Coua caerulea*), Madagascar Pygmy Kingfisher (*Ispidina madagascariensis*), and Wedge-tailed Jery (*Hartertula flavoviridis*). On two occasions, a territorial male performed the wing-flap pump in response to our arrival at its territory early in the morning.

Preening.—Territorial males preen their plumage with their bills and

feet persistently throughout the day. Preening was observed in 128 5-min observation periods (23% of observation periods, or 36% of observation periods in which the male was present on his territory). Preening behavior was often extensive. For example, on one occasion a male was observed preening continuously on a single perch for over 25 min. In another instance, a male seized a 1 cm-long ant and rubbed it in on body plumage for about 10 sec. No other unusual movements were associated with this "anting" behavior.

Nesting and fledgling care.—All of the more than 25 nests of *P. castanea* that have been observed at Ranomafana over the last decade were placed near the end of long overhanging branches of a single common species of forest tree: *Tambourissa obevata* (Loret Rasabo, pers. comm.; Prum and Razafindratsita, in prep). *Tambourissa obevata* has simple, entire leaves about 15 cm long with pointed "drip tips." Nest trees are frequently reused over a number of years. In November 1994, a single large tree at Ranomafana included remnants of six *castanea* nests that had been constructed on different branches in previous seasons.

The nest of *P. castanea* is a hanging sphere of moss and fine plant fibers about 25 cm long and 12 cm wide. Nest construction and fledgling attendance were observed on several occasions by Razafindratsita in the 1993–1994 breeding season. Three partial or complete nests were observed in late November and December 1993 (C-125, C-275, and F-0). Construction was observed at the C-125 and C-275 nests. Each nest was built by two female-plumaged birds that were closely associated with one another and frequently perched within one m of each other near the nest. One of the pair of individuals at the C-125 nest in 1993 was certainly female since it was banded in female plumage in 1991. Nests were built over more than ten days. One nest that was nearing completion on 27 November 1993 had no eggs inside on 8 December 1993. No nests were found in November 1994.

Nests were not placed in known male territories, but adult males were observed in the vicinity of two nests. One male was observed exiting from the C-125 nest on 26 November 1993, and associating briefly with the two female-plumaged birds. An adult male was also observed in association with two female-plumaged birds near the C-275 nest on one occasion. This male called and chased the two female plumage birds. These males, however, were not consistently associated with these nests, and were not observed constructing the nests.

A single female-plumaged bird was observed attending a group of three dependent fledglings for one hour by Razafindratsita on 26 January 1994 at C-300, just 25 m from one nest observed in the previous month. The fledglings had female-like plumage but were distinguished by having few-

er stripes below, shorter tails, and conspicuous yellow gape marks. The three fledglings begged and chased the presumed female. The female-plumaged bird foraged for fruits and placed them whole in the mouths of the begging young.

Diet.—The diet and ecology of *P. castanea* is being studied intensively at Ranomafana by V. R. Razafindratsita and S. Zack (in prep.). Their observations confirm that *castanea* is extensively frugivorous. However, our observations during November 1994, when the weather was unusually dry and fruit was extremely scarce, indicate that nectar feeding is a seasonally important food source for *castanea.* Of particular importance is *Bakerella*—a common parasitic mistletoe (Loranthaceae) with abundant, bright pink flowers (See Frontispiece). Male UB#3 was observed foraging on the *Bakerella* nectar on 12 occasions during ten observation days in late November 1994.

Salomonsen (1965) states that the tongue of *castanea* is unspecialized for nectar feeding. However, observations of the tongues of spirit specimens show that the tongue of *P. castanea* is bifid distally, and that each side is divided into numerous, fine brushy tips, as found in other nectarivorous birds (FMNH 345696-7, 345708-10).

Annual cycle.—Langrand (1990) states that nesting has been observed from August through January, but this includes records from the entire range of *castanea.* At Ranomafana, *P. castanea* breeds between November and February. Nest construction was observed in November and December 1993, and fledgling attendance was observed on 26 January 1994. The beginning of the 1994–1995 breeding season was apparently delayed. Territorial males were not encountered until 20 November 1994 and no nest were observed by the end of the month. This delay may have been due to the unusually extended dry season at this locality in November 1994.

Further north in Madagascar, breeding occurs earlier in the year (Lambert and Woodcock, in press). For example, Rand (1936) reports collecting a nest with eggs and specimens of males and females in breeding condition in late August and early September west of Andapa. The initiation of breeding across Madagascar appears to follow the arrival of the spring rainy season.

The acquisition of breeding aspect and the development of caruncles also varies with latitude. In northern Madagascar, most adult males acquire worn basic plumage and complete caruncles by August-September, and some as early as late June (Rand 1936, specimens in AMNH). In five breeding seasons at Ranomafana, >90% of male Velvet Asity have acquired entirely black appearance and caruncles by October (S. Zack, pers. comm.). However, in 1994, all males observed in early November had

extensive yellow-green feather edgings of the nonbreeding aspect of the male definitive basic plumage. Most adult males were in transition from green to black appearance (showing partial remnants of yellow-green edgings) throughout the month of November.

DISCUSSION

Breeding system of Philepitta castanea.—Our field observations of *Philepitta castanea* indicate that this species breeds in a display polygyny system. Males apparently occupy non-resource based territories that are distributed in dispersed leks. Males defend these territories from other males, and perform elaborate, secondary sexual displays. The display repertoire includes both intersexual courtship elements (the erect posture and wing-flap pump display) which are performed during male–female interactions, and intrasexual competitive elements (the horizontal posture, open gape, and hanging gape displays) which are performed during male–male competitive interactions. At least some male territories are occupied in successive breeding seasons, probably by the same males (Table 1). Male display territories lack resources necessary for reproduction. They are too small to include significant food resources, and even territorial males leave the territory frequently to forage. Furthermore, three nests observed during these observation periods were not placed within any male territories. Indeed, two nests observed in December 1993 (at C-125 and C-275) were 100 and 50 m, respectively, from the territory of male UB#4/GWOO (at E-10). This male remained on its display territory consistently throughout the day during the construction and attendance by female-plumaged birds at these two nearby nests. Lastly, five male territories lacked any individuals of the tree species in which *P. castanea* exclusively nests at this locality.

Although most males appear not to develop pair bonds with females during the breeding season, single adult males were observed near nests in association with female-plumage birds on several occasions. These males were not consistently present at these nests and took no part in nest construction or parental care. However, some males in the population may establish a pair bond or social association with females outside of the display territory system. Further, Langrand (1990) states that both parents feed the young, but this conclusion has not been documented. Thus, *P. castanea* may be characterized by significant behavioral plasticity among males.

Even with this small sample of observations, some of the display elements of *castanea* appear to be quite variable. For example, two males performed the wing-flap pump display in strikingly different fashion. Such ethological variation is unknown in most polygynous birds (e.g.,

manakins, Prum 1990) with some conspicuous exceptions (e.g., Ruff, *Philomachus pugnax*; Rhijn 1973).

An additional peculiarity is the independent observations at multiple nests of two female-plumage birds during nest construction. Cooperative breeding currently is known in few species of frugivorous passerine (Brown 1987). It seems likely that both female-plumage individuals observed at the nests were actually females. It is possible, however, that the additional female-plumage birds were predefinitive males that are pursuing an alternative breeding strategy. More detailed observations of multiple territorial males and nests throughout entire breeding seasons are required to further understand the nature of the breeding system and behavioral variation of *P. castanea.*

Evolution of breeding systems, display behavior, plumage, and diet of the asities.—Little is known about the breeding systems of the three other species of asity (Lambert and Woodcock, in press). Schlegel's Asity (*Philepitta schlegeli*) is restricted to deciduous dry forests of northwestern Madagascar (Langrand 1990). A recent observation of nest construction in *schlegeli* indicates that a male and female have a pair bond and construct the nest together (Hawkins 1994). However, other observers have encountered 6 male *schlegeli* calling simultaneously from separate perches spaced along 150 m of trail during the breeding season, in a spatial pattern reminiscent of dispersed leks (P. Morris and B. Wright, pers. comm.). Additional observations are required to determine whether *schlegeli* populations exhibit polygyny or variation in breeding system. In the Common Sunbird Asity (*Neodrepanis coruscans*), there is a pair bond between the sexes, but the nest is constructed entirely by the female (Prum and Razafindratsita, in prep.). Similarly, in the Yellow-bellied Sunbird Asity (*Neodrepanis hypoxantha*), there is a pair bond with female-only nest construction (S. M. Goodman, F. Hawkins, and M. Putnam, pers. comm.).

Several elaborate display elements have been observed in other species of asities. A male *P. schlegeli* was observed displaying next to a female by "drooping his wings, fluffing up breast feathers and lifting his tail so that it almost touched his rump feathers" (Hawkins 1994). This display appears to be unique among asities; none of the details of this tail-cocked posture appear to be homologous with the display elements of the congeneric *P. castanea* (Fig. 7). However, male *N. hypoxantha* have been observed performing a display in which the male leans forward with its body held below the perch with its tail held above the perch, the throat feathers fluffed, and the bill and head held horizontal; in this posture the male flicks his wings and vocalizes energetically (S. M. Goodman, F. Hawkins, and M. Putnam, pers. comm.; F. Hawkins, photograph). This

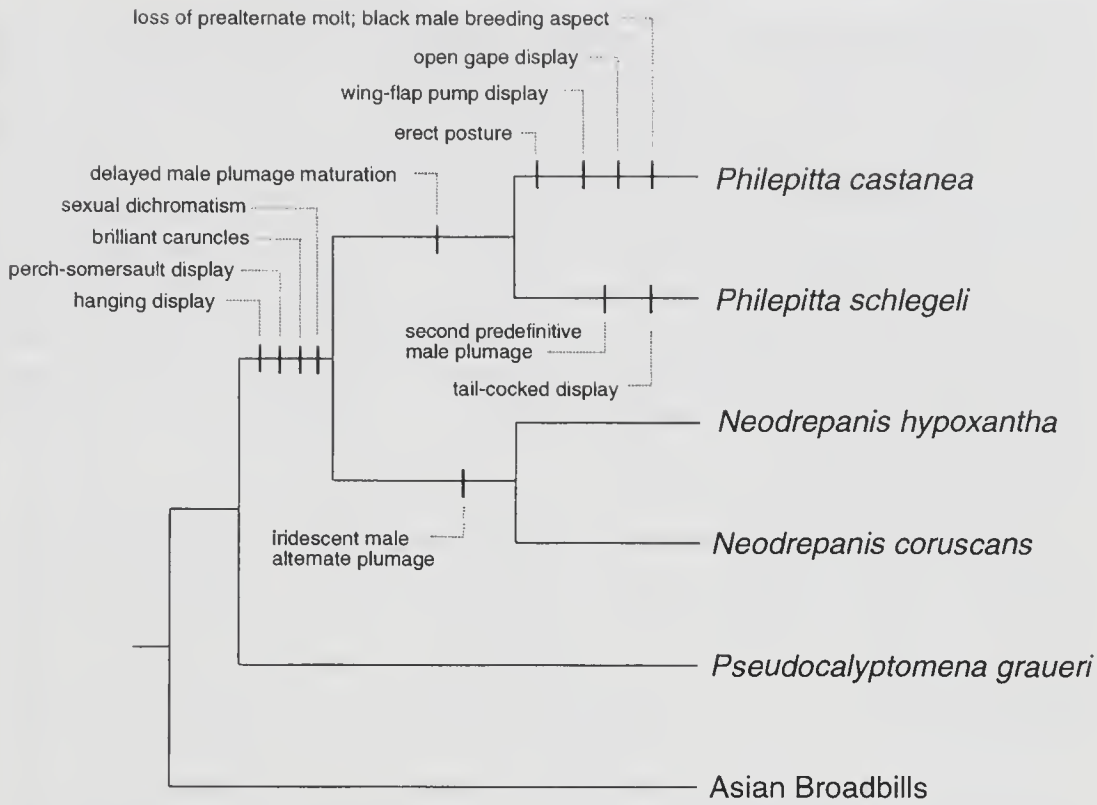

FIG. 7. Phylogenetic patterns in the evolution of display elements and plumages of the asities. Tick marks indicate the lineages during which various traits are hypothesized to have originally evolved (see Discussion; relative position of trait changes on a single lineage is arbitrary). The phylogenetic hypothesis is based on morphology (Prum 1993). The sister group to the asities is the African Green Broadbill *Pseudocalyptomena graueri*; the sister group to this group is a clade including Asian broadbills except *Calyptomena* (Prum 1993).

display is extremely similar to the hanging gape display performed by male *castanea* (Fig. 6). In addition, a male *hypoxantha* has also been observed doing a repeated perch-somersault display while fluttering its wings in response to playback (P. Morris, pers. comm.). This display element is also extremely similar to the perch-somersault display of *castanea.*

The detailed similarities between the hanging display and perch somersault displays of *castanea* and *hypoxantha* support the hypothesis that these two display elements are behavioral homologs that originally evolved in the common ancestor of the asities, prior to the differentiation of *Neodrepanis* and *Philepitta* (Fig. 7). The detailed similarities between these displays make the alternative hypothesis of convergence unlikely. This evidence supports the prediction that a similar, homologous display element is performed by *P. schlegeli* and *N. coruscans,* or that it has been lost in these species. Since the origin of these display

elements in the common ancestor of asities, the displays have continued to evolve. Thus, a male *hypoxantha* shivers its wings and fluffs out its throat throughout the hanging gape display, whereas male *castanea* holds the gape open broadly and calls; a male *hypoxantha* flutters its wings and somersaults repeatedly, while the homologous display of *castanea* is simpler. These novel differences have probably evolved subsequent to the origin of these display elements. Interestingly, the open gape display appears to be an evolutionarily novelty that has been added to the hanging display in *castanea.* Although the hanging gape display looks like an elaboration of the open gape display, the opposite conclusion appears to be correct.

During the breeding season, all species of asities are sexually dichromatic and have brilliant, secondary sexual caruncles. Sexual dichromatism apparently evolved in the original common ancestor of the asities (Fig. 7; Prum 1993). All asities except *castanea* have two annual molts- the prebasic and the prealternate- and sexually monomorphic, basic (nonbreeding) plumages. Primitively within the asities, sexual dichromatism is achieved by the sexually dimorphic, alternate male plumage which is produced by the prealternate molt. The primitive male alternate plumage in asities was probably yellow below and green above. *Neodrepanis* subsequently evolved the iridescent blue upper parts in the male alternate plumage.

In contrast to other asities, *P. castanea* has lost the prealternate molt and has evolved a unique, sexually dimorphic basic plumage. The fresh, nonbreeding male basic plumage is scaley green. The novel, black, male appearance during the breeding season is a worn basic plumage. Thus, the beautiful, breeding aspect that gives the Velvet Asity its English name has evolved through the derived loss of the prealternate molt that was primitively present in the asities (Fig. 7). The seasonal variation in sexual dichromatism found in male asities is rare in tropical passerines, but the type of annual molt and plumage wear found in *castanea* may be unique among all tropical passerines.

The brilliant colors of the caruncles of *castanea* and other asities are produced by constructive reflection, or interference, of incident light by highly ordered collagen lattices in the dermis; this structural color mechanisms is apparently unique among animals (Prum et al. 1994; Prum, in prep.). These multicolored caruncles have also differentiated extensively among the species of asities since their origin in the common ancestor of the group (Prum 1993; Prum et al. 1994). The size, shape, colors, and surfaces textures of the caruncles vary among species. Further, the ultrastructural organization of collagen fibers has continued to evolved. In *castanea,* the arrangement of collagen fibres is much more orderly than

in either species of *Neodrepanis,* resulting in more vivid, brilliant color production (Prum et al. 1994; Prum, unpubl. date). No histological specimens exist of the caruncles of *P. schlegeli.*

Both species of *Philepitta* also have delayed male plumage maturation. In *castanea,* the predefinitive male plumage resembles female plumage. Males acquire definitive plumage and caruncles in the same season. Interestingly, since *castanea* has only a single annual, prebasic molt, the first definitive plumage acquired by any male is the basic plumage in the non-breeding season. The first male caruncles are apparently developed prior to the subsequent breeding season. However, in *schlegeli,* there are two stages, or probable age-classes, of predefinitive males. The first stage has female-like plumage and lacks caruncles as in *castanea*; the second stage-class has female-like, predefinitive plumage but has completely developed caruncles, as in the definitive male. The third stage-class has the definitive male plumage and caruncle morphology. The second stage-class, predefinitive male *schlegeli* have been observed singing like definitive males (P. Morris and B. Wright, pers. comm.). The age at which predefinitive males assume definitive adult plumage is unknown in either species of *Philepitta.*

Delayed plumage maturation originally evolved in the common ancestor of *Philepitta* with the retention of a female-like, predefinitive male plumage (Fig. 7). Delayed plumage maturation continued to evolve after its origin with the evolution of a second, distinct stage-class of predefinitive males in *schlegeli* (Fig. 7). Natural or sexual selection on the function of predefinitive plumages as social signals apparently led to the diversification of new status or age-indicating morphologies. Our limited observations indicate that predefinitive male *castanea* enter adult male territories more frequently than definitive adult males. Predefinitive male plumages may have evolved by selection to reduce the costs to young males of male-male aggression, and allow access and experience at male display sites. McDonald (1993) and Collis and Borgia (1993) have found evidence for this hypothesis in the polygynous manakins and bowerbirds, respectively.

Prum (1993) hypothesized that the primitive diet within the asities was frugivory and that nectarivory was derived in the genus *Neodrepanis.* However, observations of significant nectarivory by *castanea* at Ranomafana and our observations of the tongue morphology of *castanea* indicates that *castanea* is significantly more nectarivorous than hypothesized by Salomonsen (1965). Facultative nectarivory probably evolved in the mainly frugivorous common ancestor of the asities (Fig. 7). Extensive nectarivory in *Neodrepanis* evolved subsequently through specialization on nectar and the loss of frugivory within a

diverse, diet (Fig. 7), rather than the adoption of an entirely new food source (Prum 1993).

Conclusions.—The evolution of the numerous secondary sexual characters in the asities has likely been influenced by intersexual selection. The extreme sexual dichromatism in *castanea* is likely to be a derived, evolutionary consequence of the intense intersexual selection that occurs in lek display polygyny breeding systems. The numerous striking similarities between *P. castanea* and the polygynous/lekking manakins (Pipridae), cotingas (Cotingidae), birds of paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae) first lead us to initiate this study of its breeding system. As hypothesized by Snow (1971, 1976), frugivory, in combination with nest predation, can result in the evolutionary "emancipation [*sic*]" of males from parental care. This change establishes the opportunity for female mate choice, and can initiate the evolution of elaborate sexual dimorphism, intersexual display behavior, and lek behavior.

Although more observations are required, *P. castanea* is apparently the first known lekking bird in Madagascar. *P. castanea* belongs with the manakins, cotingas, birds of paradise, bowerbirds, hummingbirds, and others as another, phylogenetically independent example in support of the relationship between diet, parental care, and the evolution of lek behavior proposed by Snow (1971, 1976). Further, natural and sexual selection have lead to coherent phylogenetic patterns in the evolution of display elements in asities that are similar to those of the Neotropical manakins (Pipridae; Prum 1990). *P. castanea* constitutes an extreme example of the behavioral diversity within the Old World suboscine clade, and further substantiates this group as a premier example of avian evolutionary radiation that deserves further study.

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COLOR PLATE

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INFLUENCE OF AGE AND PREY AVAILABILITY ON BALD EAGLE FORAGING BEHAVIOR AT GLACIER NATIONAL PARK, MONTANA

ROBERT E. BENNETTS[1,2] AND B. RILEY MCCLELLAND[3,4]

ABSTRACT.—It has been hypothesized that foraging tactics and ability of Bald Eagles (*Haliaeetus leucocephalus*) are influenced by age, phenotype, and prey availability. We studied the influence of eagle age class and prey availability of kokanee salmon (*Oncorhynchus nerka*) on foraging behavior of Bald Eagles during autumns of 1983 and 1984 at Glacier National Park, Montana. The relative use of foraging tactics differed among four age classes of eagles during both years. Stooping was the most successful tactic and was most frequently used by older birds. The relative use of stooping increased with age and the use of ground piracy tended to decrease with age. The relative use of different foraging tactics also reflected changing prey availability. During 1983, when lower numbers of salmon precluded accumulation of carcasses, eagles rarely used ground tactics (i.e., scavenging and ground piracy). In 1984, when salmon carcasses accumulated in large numbers, all age classes used ground tactics, which became the predominant foraging method of younger eagles. Our results support the hypotheses that the ability to obtain food increases with age and that eagles forage by methods for which their age class is most suited based on morphology (e.g., size and wing loading) and experience. *Received 30 Sept. 1996, accepted 1 Feb. 1997.*

During the autumns of 1983 and 1984 we assessed the influences of age and prey availability on foraging methods and prey capture success of Bald Eagles in Glacier National Park (GNP), Montana. The foraging ecology of wintering Bald Eagles has been the focus of previous studies (e.g., Stalmaster and Plettner 1992, Brown 1993); however, the concentration of Bald Eagles at GNP offered several unique characteristics. Bald Eagle concentrations based on prey other than salmon (e.g., Stalmaster and Plettner 1992, Brown 1993) usually consist of multiple prey types and habitats which can confound assessments of the influence of prey availability. In contrast, the food resource for Bald Eagles at GNP was almost exclusively a single species, kokanee salmon (*Oncorhynchus nerka*), of one age class (spawners mostly four years old). Fish varied greatly in abundance and vulnerability to capture among and within seasons (McClelland et al. 1982, Bennetts and McClelland 1991). Consequently, we were able to assess the influence of prey availability on the foraging

[1] Division of Biological Sciences, Univ. of Montana, Missoula, Montana 59812.
[2] Present Address: Florida Cooperative Fish and Wildlife Research Unit, P.O. Box 110450, Univ. of Florida, Gainesville, Florida 32611-0450.
[3] School of Forestry, Univ. of Montana, Missoula, Montana 59812.
[4] Present Address: P.O. Box 366, West Glacier, Montana 59936.

tactics and success of Bald Eagles in an environment that minimized confounding variation. Also, in contrast to most other eagle concentrations based on spawning salmon, the salmon at GNP were small enough to be carried in flight by eagles. At other salmon-based concentrations (e.g., Stalmaster and Gessaman 1984, Hansen 1986, Knight and Skagen 1988), the potential for eagles to use aerial attacks (e.g., stooping or aerial piracy) to capture salmon was largely precluded because of the large size of salmon. Consequently, a broader spectrum of foraging methods was possible at GNP compared to other salmon-based concentrations.

Previous studies on the effects of age on eagle foraging ecology generally have assigned birds to one of two age classes (adults and immatures). Because Bald Eagles usually require ≥4.5 years to acquire definitive plumage (McCollough 1989), grouping all immatures together combines several different age classes. Thus, the development of foraging ability from juvenile through several subadult stages may be masked. We assessed the influence of relative age on foraging ecology based on four age classes and could, therefore, more effectively evaluate how foraging ability changes with age.

STUDY AREA AND METHODS

GNP (approximately 48°30′N, 114°00′W) is adjacent to the Canadian border in northwestern Montana and is bisected by the Continental Divide. Beginning in the late 1930's, Bald Eagles were attracted to non-native spawning kokanee salmon in Lower McDonald Creek (LMC) in GNP. An annual concentration of Bald Eagles persisted until 1986, when the salmon population began a precipitous collapse (Spencer et al. 1991). LMC flows 4 km from the outlet of Lake McDonald to the confluence with the Middle Fork of the Flathead River. The average width of LMC during the autumn is approximately 25 m; it is interspersed with deep pools, shallow runs with gravel beds, and riffles.

Bald Eagles at LMC were counted weekly during both years using the procedures described by McClelland et al. (1982). These counts were standardized to enable meaningful comparisons among and within years, and were designed to minimize the chance of repeatedly counting the same birds.

Age classes.—Eagles were assigned to one of four age classes based on plumage characteristics subsequently described by McCollough (1989). Our juvenile age class corresponded to the "Juvenal Plumage" described by McCollough (1989) for birds one-half year old. Early subadults corresponded to the "Basic I" and "Basic II" plumage classes for birds that were 1½ and 2½ years old, respectively. Late subadults corresponded to the "Basic III" plumage class for birds that were 3½ years old. Eagles appearing to have a completely white head and tail were classified as adults, corresponding to McCollough's (1989) "Basic IV" and "Definitive" plumage classes for birds that were 4½ and >4½ years old, respectively. We did not attempt to distinguish between Basic IV and definitive plumage classes or between Basic I and Basic II classes because of the potential for errors under field conditions.

Prey availability.—Prey availability was assessed both quantitatively and qualitatively. Salmon counts were conducted bi-weekly by Montana Department of Fish, Wildlife, and Parks (MDFWP; Fraley and McMullin 1983, Fraley 1984). Two biologists snorkeled LMC, independently estimating the number of live salmon at each pool, run, and riffle; the two

counts were averaged for a final estimate. Although not conducted consistently, MDFWP biologists also counted numbers of dead salmon when conditions allowed. Descriptive accounts of spawning behavior also were recorded during these counts. Based on studies of tagged individuals, the residence time of individual salmon at LMC was estimated to be 6–8 weeks (Fraley 1984). During this time kokanee exhibited four major behavioral phases: (1) courtship, (2) redd construction, (3) egg deposition, and (4) redd maintenance (Fraley and McMullin 1983). Speculating that these spawning phases and the corresponding changes in physical condition of the salmon influenced their availability to eagles, we assigned each two-week time period (with the bi-weekly count as midpoint) to a spawning phase based on the predominant spawning behavior occurring during that period. We also included one additional phase representing the time period after spawning behaviors ceased. Spawning phases were characterized as: *(1) Courtship*—When kokanee first arrived they were in strong physical condition. They congregated in deep pools and generally were unavailable to eagles. This activity occurred primarily before eagles began congregating in large numbers; therefore, it was not included in our sample of foraging observations. *(2) Redd construction*—Some salmon ventured into shallower water and began constructing redds. Salmon remained in good physical condition, but spawners in shallow water became vulnerable to aerial attacks by eagles. About 10% of the salmon deposited eggs during this phase. *(3) Egg deposition*—Egg deposition peaked and most salmon were in some stage of spawning, where they were highly vulnerable to stooping attacks by eagles. Physical condition of salmon deteriorated after spawning. Dead salmon became available for scavenging, but live salmon provided more foraging opportunities. *(4) Redd maintenance*—Live salmon still outnumbered dead salmon, but almost all were in severely weakened condition. Numbers of dead salmon peaked during this phase and carcasses typically accumulated. Salmon were vulnerable to all foraging tactics. *(5) Post spawning*—Few live salmon remained. Dead and dying salmon were rapidly taken by eagles or other scavengers (e.g., grizzly bears [*Ursus arctos*]). Remaining carcasses accumulated only in deep pools, where they were unavailable to eagles.

Foraging methods.—Data were collected four days per week during the autumns of 1983 and 1984 from two viewing areas (previously described by Bennetts and McClelland [1991]) along LMC. Three two-hour observation periods were conducted each day; periods alternated between viewing areas. The morning observation period began 30 min after sunrise. The evening period ended 30 min before sunset; a mid-day period was mid-way between the morning and evening periods.

Foraging attempts were characterized as (1) stooping, (2) scavenging, (3) aerial piracy, or (4) ground piracy. We defined stooping as an eagle coming to within 1 m of the water surface during a dive that was initiated from either a perch or the air. Stooping was directed at live or floating dead salmon. When scavenging, an eagle walked or waded to an unattended dead salmon. In aerial piracy, a pursuing eagle came within 1 m of a flying eagle carrying a salmon (Bennetts et al. 1990). Ground piracy occurred when an eagle attempted to steal from another eagle on the ground. Initiation of this foraging method was from the ground, air, or a perch. We distinguished between aerial and ground piracy because these foraging tactics required different skills. For each attempt, we recorded the age class of the foraging eagle, foraging method, and whether the bird was successful.

Foraging success.—We used two measures of foraging success. First, we measured foraging success on a per-attempt basis. We considered an attempt successful if the foraging bird maintained possession of the prey item for at least 15 s. Scavenging could not be included in this analyses; by definition, the act of walking or wading to an unattended prey item resulted in a successful attempt. Because we could not discern the motive of a bird walking or wading in the absence of a prey item, we did not attempt to classify such behavior

as a scavenging attempt. If the prey item was obtained by displacing another bird, it was piracy rather than a scavenging attempt. We did not observe more than one eagle feeding on the same fish. Fish take was estimated as the number of fish taken by a given age class per hour divided by the average number of eagles of that age class counted. A minimum of two ($\bar{x}$ = 2.9/observation period) censuses of the number of birds of each age class present in our viewing area were taken during each observation period.

Analyses.—Using log-linear models, we explored the effects of age, year, and spawning phase on the use of different foraging tactics. Because a fully saturated model (i.e., with all possible main effects and interactions) had 128 parameters, many of which were not identifiable or estimable, we began this analysis by first exploring the effect of individual first- and second-order interactions (i.e., two and three-way interactions). This is analogous to the preliminary univariate tests suggested by Hosmer and Lemeshow (1989) for logistic regression. To test these interactions we used a likelihood ratio test of saturated models (only for effects being evaluated) and the same model without the interaction being tested. Similarly, we tested main effects using a likelihood-ratio test between a full main-effects model and models lacking each main effect individually. We then used a combination of likelihood ratio tests and Akaike's Information Criteria (AIC) (Akaike 1973, Shibata 1989) to determine the most parsimonious model based on all combinations of effects indicated from our preliminary exploration. In contrast to likelihood ratio tests, which are used for pairwise comparisons of nested models, AIC is used more as an optimization tool for any number of models, nested or not. Models with AIC differences <2 were not considered as statistically significant (Sakamoto et al. 1986).

We tested the influence of age, year, spawning phase, and foraging tactic on success (per attempt) using logistic regression with success as a binary response variable. We began with a univariate analyses of each main effect. Because the potential contribution of main effects to interactions may be masked at this step, we initially used a liberal rejection criteria of $\alpha = 0.25$ (Hosmer and Lemeshow 1989). We then constructed a model including all main effects meeting the above criteria. At this and all subsequent steps of the analysis, we used a rejection criteria of $\alpha = 0.05$. We then used a combination of likelihood ratio tests and AIC to test for the inclusion or rejection of interaction terms (Hosmer and Lemeshow 1989).

We tested for the effects of age, foraging tactic, spawning phase, and year on fish take per hour using an offset log-linear model (Agresti 1990). An offset model is an extension of a log-linear model in that the number of fish for a given cell is modeled as a function of their exposure (risk) to eagles such that: $\log(f_{ij}/E_{ij}) = \beta_0 + \beta_1 \ldots \beta_k$, where f_{ij} is the number of fish captured for a given cell, E_{ij} is the exposure (total eagle hours from censuses), β_0 is the intercept, $\beta_1 \ldots \beta_k$ are the main effects (i.e., age, year, tactic, and spawning phase) plus any interaction effects.

RESULTS

Prey availability.—Salmon began arriving at LMC in September of both years; however, eagles did not begin to congregate in large numbers until October and November (Fig. 1). The peak salmon count was substantially lower in 1983 (34,200) than in 1984 (86,500) and occurred approximately two weeks earlier in 1983. During both autumns, the peak abundance of live salmon occurred during the redd construction phase. During 1983, the highest number of dead salmon (2870) was counted during the redd maintenance phase, when peak accumulations probably occurred. The lower number of salmon and rapid consumption by pred-

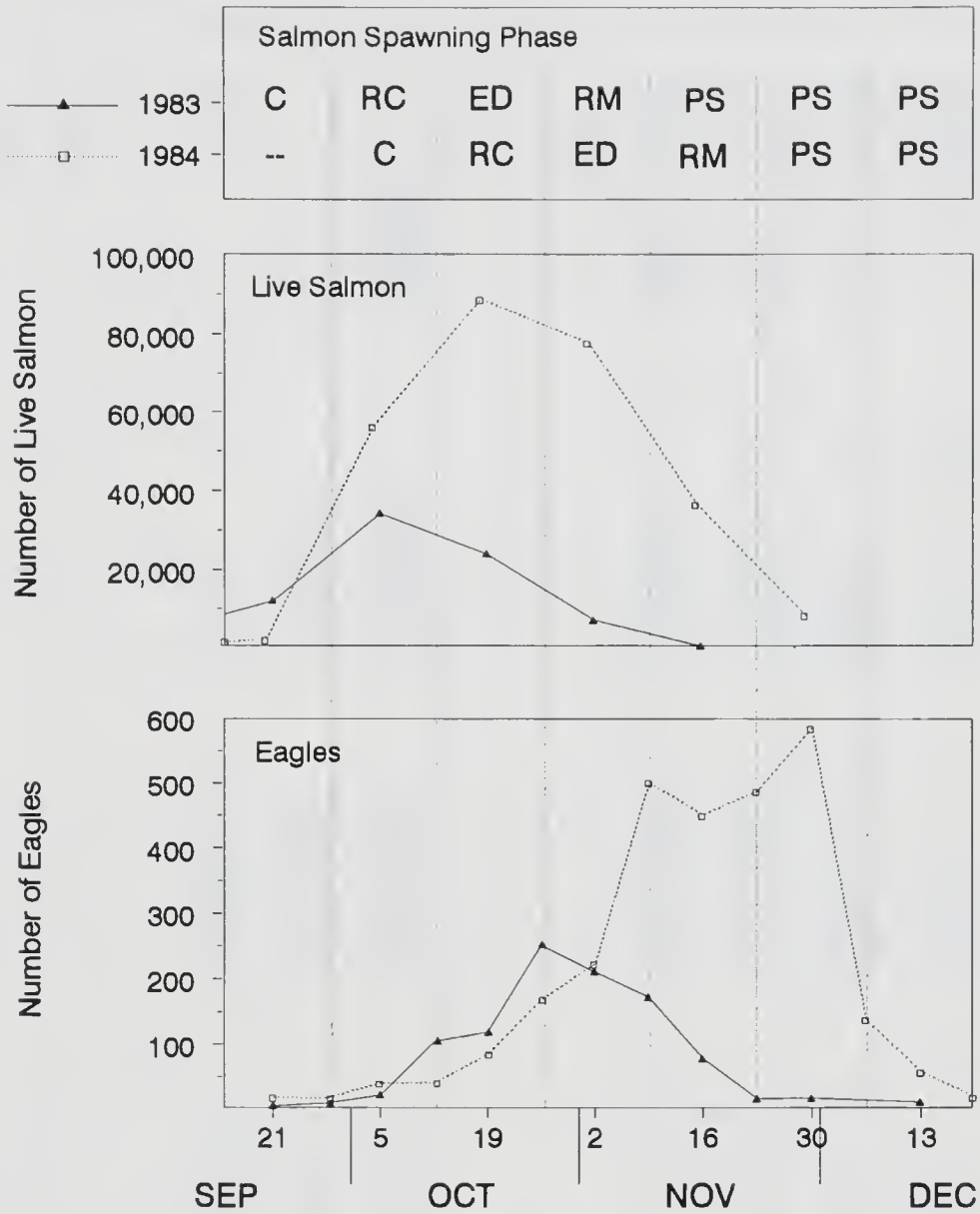


FIG. 1. Spawning phase, number of live salmon, and number of eagles counted during each two-week time period of this study. Salmon spawning phases were courtship (C), redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

ators and scavengers largely precluded accumulations of salmon carcasses in 1983. During 1984, the peak count of dead salmon (4500) occurred during the egg deposition phase, approximately two weeks prior to peak accumulations. High numbers of live salmon and decomposition of carcasses precluded counting dead salmon during the latter part of 1984. Thus, peak numbers of dead salmon in 1984 were unknown, but were >4500 and substantial accumulations of carcasses were readily apparent.

Foraging methods.—We observed 1485 foraging attempts by Bald Ea-

TABLE 1

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) LOG-LINEAR MODEL OF THE INTERACTIONS BETWEEN FORAGING TACTICS AND AGE, YEAR, AND SPAWNING PHASE BY BALD EAGLES

Source	χ^2	df	Prob > χ^2
Age[a]	271.25	3	<0.001
Tactic[a]	92.75	3	<0.001
Year[a]	37.12	1	<0.001
Phase[a]	30.94	3	<0.001
Tactic*Age	187.50	9	<0.001
Tactic*Year[b]	7.55	3	0.056
Tactic*Phase	62.76	9	<0.001
Tactic*Year*Phase[c]	63.74	4	<0.001

[a] Log-linear models are intended to detect interactions; however, main effect terms were retained to account for marginal totals.

[b] Model selection procedures indicated similar fit of models with and without this term. We retained this term to better account for its contribution to the three-way interacion.

[c] We did not have any observations during the redd construction phase of 1983; thus, some cells had structural zeros.

gles at LMC (301 during 1983 and 1184 during 1984). Our final log-linear model indicated that the foraging tactics used by Bald Eagles differed substantially among age classes, between years, and among spawning phases within years (Table 1) and several patterns emerged from this analysis (Fig. 2). Relative use of stooping increased with age class during both years. Younger birds correspondingly scavenged and used ground piracy more than older birds, particularly in 1984. Juveniles and early subadults also used aerial piracy more than older birds did in 1983.

One of the most pronounced differences between years was the relatively high use of ground tactics (i.e., scavenging and ground piracy) during 1984. The use of these tactics was almost completely lacking by adults and late subadults during 1983, when these tactics were used by juveniles and early subadults only during the egg deposition phase.

The relative use of stooping by younger birds tended to increase over time (i.e., among successive spawning phases) in 1983; however, use of this tactic tended to decrease over time for all age classes during 1984. The use of ground piracy by juveniles was completely lacking during the redd construction phase of 1984, but became the most frequently used tactic for this age class during later time periods.

Foraging success per attempt.—Our final logistic regression model indicated that foraging success per attempt was influenced by tactic, year, and spawning phase (Table 2). Based on a likelihood-ratio test, age had only a marginal effect on success per attempt ($\chi^2 = 5.30$, 3 df, $P = 0.15$) and AIC for models with and without an age effect also were similar

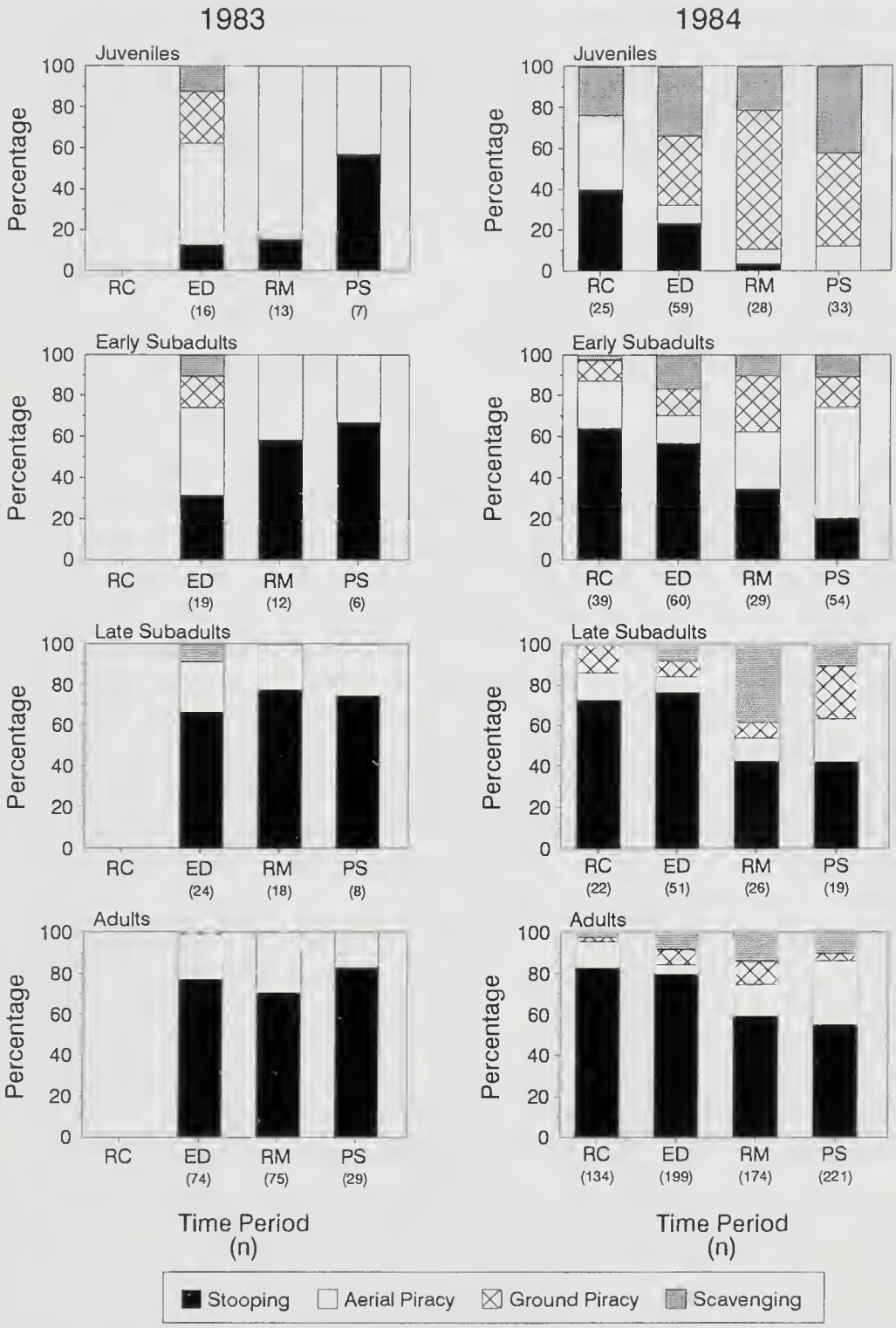


FIG. 2. Percentage use of foraging tactics by age class during spawning phases, 1983 and 1984. Salmon spawning phases were: redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

TABLE 2

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) LOGISTIC REGRESSION MODEL OF THE INFLUENCE OF FORAGING TACTIC, YEAR, AND SPAWNING PHASE ON SUCCESS (PER ATTEMPT) OF FORAGING BALD EAGLES

Source[a]	χ^2	df	Prob > χ^2
Year	6.70	1	0.009
Tactic	159.91	2	<0.001
Phase	8.65	3	0.034

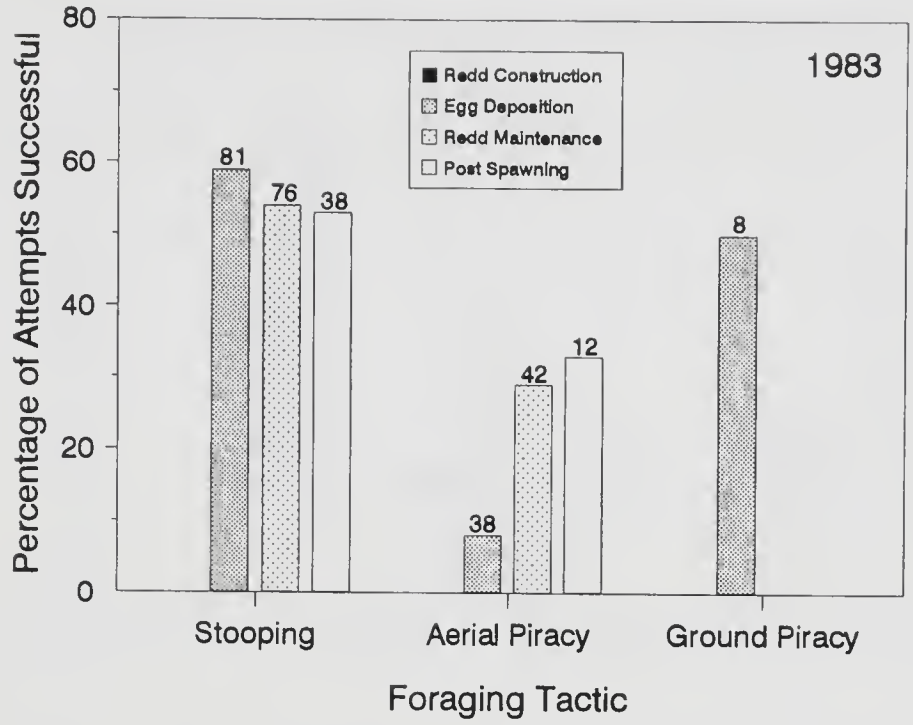
[a] Scavenging was not included in this analysis because all attempts, by definition, were successful.

(AIC = 1586.90 and 1586.20 for models with and without an age effect, respectively). Although AIC indicated that models with and without an age effect both were adequate, we did not retain an age term in our final model based on the principal of parsimony. No interaction terms were supported by our data based on either likelihood-ratio tests or AIC.

Foraging tactic had the most pronounced influence on success per attempt (Table 2). Success was highest for stooping and lowest for aerial piracy (Fig. 3). Success of stooping was generally higher in 1984 than in 1983. Variation among spawning phases occurred; however, with the exception of aerial piracy during 1983, there was no apparent systematic pattern to this variation. Except during 1983 when success of aerial piracy increased 24% over time, use of foraging tactics among spawning phases varied up to 16% in no apparent pattern.

Our analysis did not indicate a difference among age classes in foraging success per attempt. Juveniles did, however, have the lowest (albeit insignificant) success per attempt at stooping (53%) compared to early subadults (60%), late subadults (57%), and adults (68%). In addition, stooping attempts by juveniles generally were on floating dead fish in calm water. These attempts posed relatively little difficulty in comparison to submerged live fish often taken by adults.

Foraging success per hour.—Fish take per hour was influenced by age, foraging tactic, year, spawning phase, and several interactive effects (Table 3). Overall, fish take increased with age during both years, although intake for each age class was lower in 1983 than in 1984 (Fig. 4). Fish take by stooping was substantially higher than for any other foraging tactic (Fig. 5). Fish take by scavenging and by ground piracy were the next most profitable in 1984. During 1983, fish take using each of these tactics was less than by aerial piracy. During 1983, fish take increased with age for stooping and scavenging, but decreased with age for aerial piracy (Fig. 6). During 1984, fish take increased with age for stooping



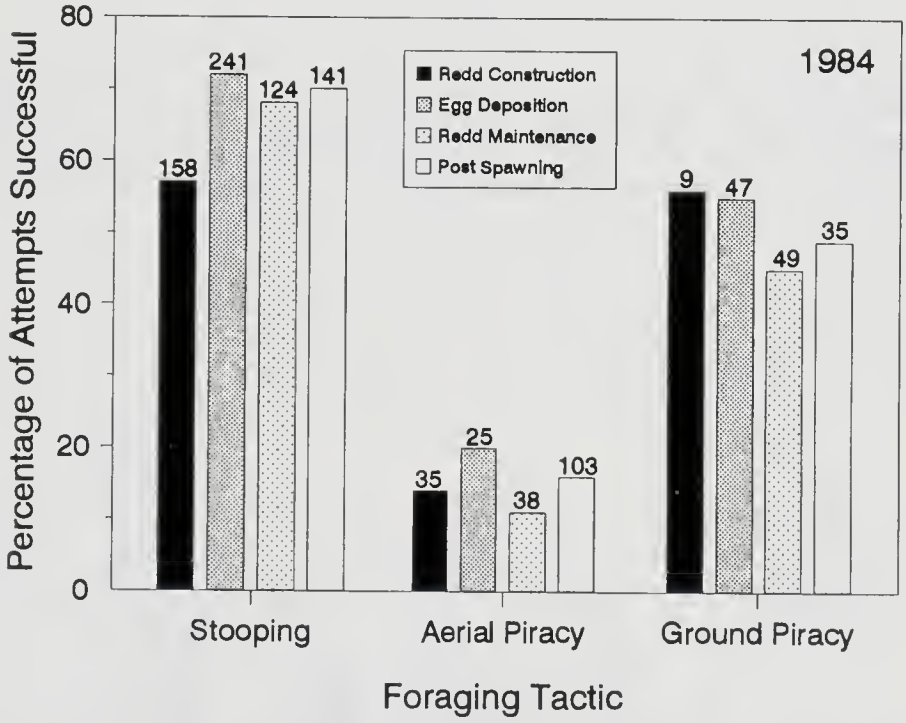


FIG. 3. Percentage of successful foraging attempts by foraging tactic and spawning phase, 1983 and 1984. Above each bar is the number of attempts on which percentage is based.

TABLE 3

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) OFFSET LOG-LINEAR MODEL OF THE INFLUENCE OF FORAGING TACTIC, YEAR, AND SPAWNING PHASE ON FORAGING SUCCESS OF BALD EAGLES MEASURED AS FOOD INTAKE PER UNIT TIME

Source	χ^2	df	Prob > χ^2
Age[a]	230.19	10	<0.001
Year[a]	119.50	15	<0.001
Tactic[a]	716.06	24	<0.001
Phase[a]	155.34	15	<0.001
Age*Tactic	99.70	9	<0.001
Age*Year	11.04	3	0.012
Tactic*Year	54.03	3	<0.001
Tactic*Phase	44.72	3	<0.001
Phase*Year	32.51	3	<0.001

[a] Because a main effects model (i.e., one model with all main effects but no interactions) did not fit the data ($P < 0.001$), significance of each main effect was determined using a likelihood ratio test between the selected model and a model lacking all terms using that main effect (including interactions). Degrees of freedom for main effects reflect this approach.

and aerial piracy, but decreased with age for scavenging and ground piracy.

During both years, fish take was highest during the egg deposition phase (Fig. 7). We did not make foraging observations during the redd construction phase during 1983 because of the scarcity of eagles during this period. Fish take decreased among each consecutive spawning phase

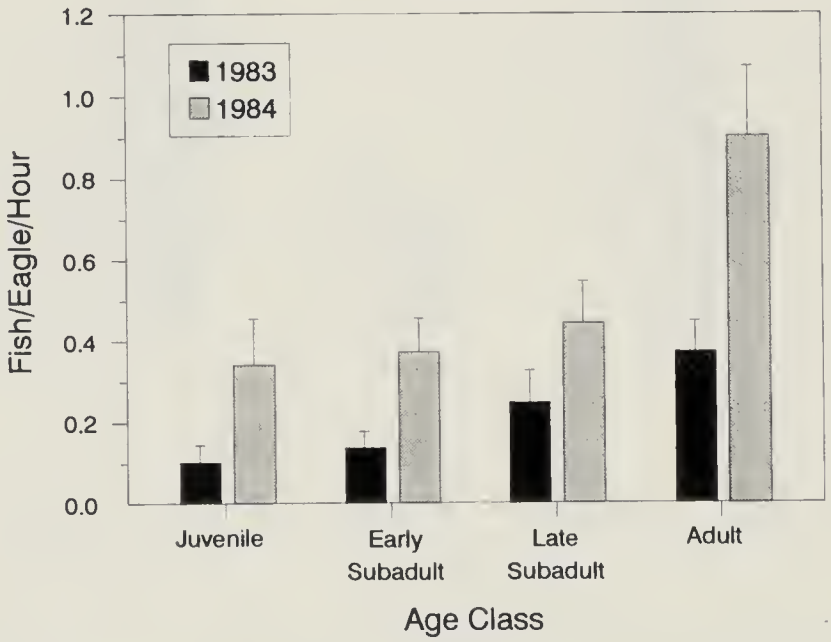


FIG. 4. Mean (+1 SE) fish take per hour by eagle age class, 1983 and 1984.

FIG. 5. Mean (+1 SE) fish take per hour by foraging tactic, 1983 and 1984.

during 1983, but showed an increase between the redd maintenance and post-spawning phases in 1984.

DISCUSSION

Influence of age on foraging behavior.—Hansen (1986) hypothesized that Bald Eagles use foraging methods for which they are phenotypically suited. Our data at LMC indicated that the ability of Bald Eagles to obtain food is dependent on their morphology (e.g., size and wing loading), experience, and possibly hunger level. Compared to younger age classes the aspect ratio, wing loading, and tail/wing ratio of adult Bald Eagles probably are better suited to the type of flight required to capture live prey (Harmata 1984). The relative use of stooping, which was the predominant and most successful method of capturing live prey at LMC, increased with age.

In addition to morphological differences among age classes, Bald Eagles may increase foraging skill through experience gained with age. Foraging methods most frequently used by younger eagles, particularly juveniles, required the least skill (i.e., ground approaches to prey rather than flying). Stooping and aerial piracy required not only detection of the prey, but also agility and precise timing, in contrast to scavenging which primarily required detection. Ground piracy probably requires more skill than does scavenging, but the host usually is stationary on the ground, often enabling even a juvenile's awkward approach to be successful. This appears to contradict Hansen's (1986) view that piracy requires more skill than hunting; however, foraging options at Hansen's study site on the

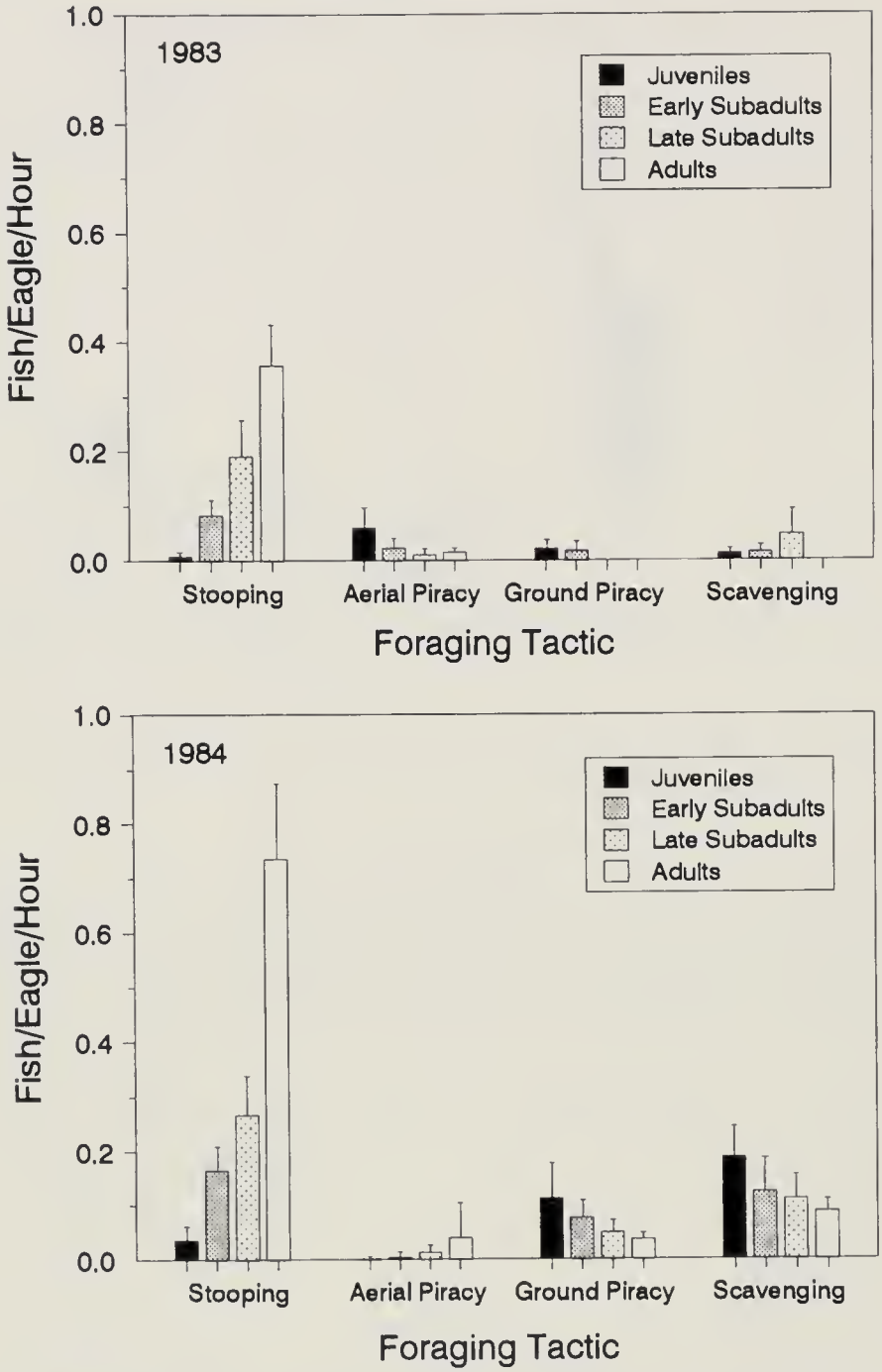


FIG. 6. The mean (+1 SE) fish take per hour by age class and foraging tactic, 1983 and 1984.

Chilkat River in Alaska differed markedly from the conditions at LMC. Salmon on the Chilkat River averaged 4.3 kg (Hansen 1986), whereas kokanee at LMC averaged 0.49 kg in 1983 and 0.33 kg in 1984 (MDFWP, unpubl. data). The larger prey on Hansen's (1986) study site precluded the use of stooping and aerial piracy or the taking of live prey. Thus,

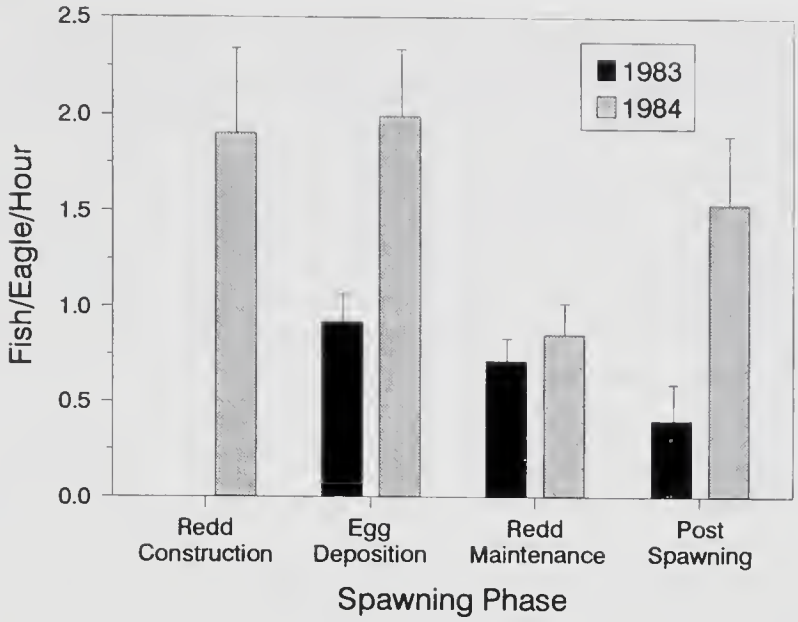


FIG. 7. Mean (+1 SE) fish take per hour by spawning phase, 1983 and 1984. Salmon spawning phases were: redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

hunting, as described by Hansen (1986), was scavenging by our definition. Given this distinction, we agree with Hansen (1986) that piracy requires more skill than scavenging. Further, Hansen (1986) and Knight and Skagen (1988) showed that size was a more important influence on the outcome of agonistic encounters than was age. Similar to hunting, however, the large size of salmon in their respective studies precluded the use of aerial foraging tactics, thus, agonistic foraging encounters were limited to ground piracy. Our observations at LMC were consistent with the view that younger birds are more likely to initiate ground piracy. However, factors other than size (e.g., maneuverability) may be more important for aerial piracy.

The lack of accumulation of carcasses during 1983 and corresponding lack of ground tactics did not allow us to assess differences in abilities of different age classes to acquire food by different methods in that year. Conditions during 1984 probably better reflected the ability of birds to obtain food under conditions when the potential for all tactics existed; during 1984, fish take using aerial tactics increased with age and using ground tactics decreased with age.

Verbeek (1977), Griffin (1981), and Fischer (1985) suggested that younger birds resort to pirating because of less skill at capturing food. We would extend their hypothesis to suggest that younger birds used ground tactics (i.e., scavenging and ground piracy) as a result of lesser skill at aerial tactics (i.e., aerial piracy or stooping). Several patterns that

we observed may, at first, appear inconsistent with this hypothesis. First, compared to other age classes, juveniles had higher fish take using aerial piracy and higher use of this tactic during 1983. We suggest this occurred because alternative foraging tactics were not available to juveniles in 1983. The lack of accumulated carcasses precluded the use of scavenging and ground piracy and we believe that juveniles lacked the ability to obtain sufficient food by stooping. Thus, aerial piracy was the only option for juveniles to obtain food at this time even though the overall fish take by this method was low. All other age classes obtained substantially more food by stooping.

Influence of prey availability on foraging behavior.—Bald Eagles shifted use of foraging methods at LMC as prey availability changed, both within and between years. Availability of salmon at LMC was influenced not only by abundance, but also by physical condition and location in the stream (e.g., deep pools or spawning sites).

During 1983, considerably fewer salmon and rapid consumption of available salmon precluded accumulations of carcasses. Consequently, the overall use of scavenging and ground piracy was considerably lower in 1983 than in 1984. Relatively few salmon carcasses were available for scavenging during the early spawning phases of 1984, but after egg deposition, salmon carcasses began accumulating rapidly, which resulted in a general trend of decreased use of stooping and increased use of scavenging and ground piracy.

During the post-spawning phase of 1984, when food had greatly diminished, older birds increased their use of aerial piracy, but they continued to forage primarily by stooping. There also was intense competition for the few dead or dying salmon that floated downstream; as weakened salmon died and floated to the surface, they were quickly taken by stooping eagles. During the post-spawning phase, each successful capture was accompanied by a flurry of aerial piracy attempts. Aerial piracy became the primary foraging method used by early subadults. We suspect this was a result of their inability to compete with adults or late subadults at stooping for the few remaining salmon. We did not quantify aerial chase parameters, but it was apparent that chases were longer in duration and more often resulted in physical contact during later spawning phases. Hansen et al. (1984) also found that the intensity of Bald Eagle aggression increased during periods of food shortage on the Chilkat River. Ground piracy and scavenging remained the primary foraging tactic for juveniles during this period, probably because they were unable to compete with older birds using stooping or aerial piracy.

Measures of foraging success.—Although we believe that our measure of fish take was reasonable for the comparisons we have made, it was a

biased estimate because we did not observe all foraging attempts; thus, our estimates of fish take should be regarded as a minimum. This could present problems if bias was not equal among comparison groups. Because adults were the most abundant age class and initiated the most foraging attempts, we would have expected to have missed more foraging attempts for this age class. The fact that our results showed fish take was highest for adults implies that our results were conservative, rather than in conflict. Similarly, time periods and years with the highest number of birds expected also occurred when fish take rates were highest. Thus, we believe that our conclusions were not exaggerated by observation bias; rather, we probably underestimated the differences among age classes or time periods.

Conservation implications.—Grier (1980) demonstrated that survival may be a relatively more important demographic influence than productivity in Bald Eagle populations. Thus, a lack of ability by younger birds to obtain food may be an important factor in survival (Stalmaster and Gessaman 1984). Our data are consistent with previous suggestions that the ability to obtain food increases with age for Bald Eagles (Stalmaster and Plettner 1992). Based on the formula presented by Stalmaster and Gessaman (1982:653), a Bald Eagle at LMC needed approximately 1.3 salmon/day in 1983 and 2.0 salmon/day in 1984 to meet minimum energy needs (differences due to disparity in mean salmon size between the two years). Adult eagles at LMC easily could have exceeded their minimum daily requirement during either year. In contrast, juveniles probably were at or below their minimum daily requirement, especially during 1983.

LMC provided older age classes of Bald Eagles with food that exceeded minimum energy requirements and we believe that younger birds benefitted as well, even though their food intake was lower than for older birds. Not only was food abundant and accessible in most years, but LMC also provided younger eagles an opportunity to observe adult foraging techniques. Because kokanee at LMC were relatively small, adult Bald Eagles used techniques requiring considerable skill not yet developed in young eagles. In both years there were approximately twice as many adults as all younger age classes combined. Before arrival at LMC, most juvenile eagles probably had little experience at foraging (McClelland et al. 1996).

If young eagles learn by observation and practice, the eagle concentration at LMC provided an exceptional opportunity for them to observe, emulate, and repeat foraging techniques used by adults. Thus, concentrations of food such as at LMC may be vital in enabling younger birds to acquire the necessary foraging skills, as well as being an important source of energy reserves for all age classes. Unfortunately, many salmon runs

throughout the Pacific Northwest, including the salmon run on which this study was based, have been devastated as a result of overfishing, habitat destruction, and mismanagement (Stalmaster 1987, Spencer et al. 1991).

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EFFECTS OF MACROHABITAT AND MICROHABITAT ON NEST-BOX USE AND NESTING SUCCESS OF AMERICAN KESTRELS

RONALD W. ROHRBAUGH, JR.[1] AND RICHARD H. YAHNER[1]

ABSTRACT.—We studied the nesting ecology of American Kestrels (*Falco sparverius*) in Berks and Lehigh Counties, Pennsylvania, from 1987–1991. Kestrels used 99 (76%) of 130 nest boxes dispersed throughout a 1000-km^2 study area. A total of 259 nesting attempts was noted: 67, 53, 49, 35, and 55 in 1987, 1988, 1989, 1990, and 1991, respectively. Of the 259 nesting attempts, 124 (49%) successfully fledged at least one offspring. We measured five macrohabitat and 14 microhabitat variables at the 130 nest boxes. Ten (53%) variables were correlated to levels of nest-box use and nesting success. Kestrels most frequently used nest boxes with high nestling-light intensity ($P = 0.02$) and low nest-box concealment ($P = 0.05$). Frequently used boxes were associated with extremely open habitat dominated by herbaceous vegetation ($P < 0.005$). Nesting kestrels avoided using boxes associated with dense habitats, such as late-successional old fields. Frequently used nest boxes were farther from forested areas than unused boxes ($P = 0.05$). Nest boxes with southeast orientations were used more frequently than expected ($P < 0.025$), and all other orientations were used in proportion to availability. Kestrels had the greatest nesting success when using nest boxes with high selection-light intensities ($P = 0.05$). Received *12 Dec. 1996, accepted 25 Mar. 1997.*

Kestrels readily use nest boxes, suggesting that paucity of natural nest sites (i.e., tree cavities) may limit breeding populations (Brauning 1982, 1992; Dahmer et al. 1984; Wheeler 1992). In several cases, the number of breeding pairs of kestrels has been shown to increase locally following the installation of boxes (Hamerstrom et al. 1973, Toland and Elder 1987, Smallwood and Collopy 1993). Natural nest cavities located within suitable breeding territories may become more limiting as habitat area and quality decline because of intensive agricultural practices and residential and commercial development. Thus, installation of nest boxes in suitable habitats where nest cavities are limiting may be increasingly important to maintain stable populations of kestrels.

Bortolotti (1994) identified the need for research concerning the influence of nest-site parameters on the breeding biology of kestrels using nest boxes. Because of the paucity of research in this area, it is not known if nest-site parameters can have detrimental effects on kestrels by increasing rates of abandonment, predation, or adult mortality. Nest boxes should be placed in habitats that promote successful reproduction as well as box

[1] School of Forest Resources, The Pennsylvania State Univ., University Park, Pennsylvania 16802-4300 (present address of Rohrbaugh: Cornell Laboratory of Ornithology, 159 Sapsucker Woods, Cornell Univ., Ithaca, New York 14850).

occupancy; however, quantitative management guidelines regarding the placement of nest boxes in such habitats have not been published.

Nest sites presumably are selected on the basis of habitat characteristics associated with the nest box and the immediate vicinity (Balgooyen 1976, 1990; Brauning 1982, 1983; Raphael 1985; Curley et al. 1987; Toland and Elder 1987). Previous studies have examined macrohabitat and microhabitat characteristics relative to nest-site selection in kestrels, but few have considered these characteristics simultaneously or related them to nesting success.

We evaluated macrohabitat and microhabitat characteristics associated with 130 nest boxes placed for American Kestrels and related these characteristics to nest-box use and nesting success. Our specific objectives were to (1) determine frequencies of nest-box use and rates of nesting success at nest boxes used by kestrels during a 5-year period, and (2) compare frequencies of nest-box use and rates of nesting success with macrohabitat and microhabitat characteristics associated with nest boxes used and unused by kestrels.

STUDY AREA AND METHODS

We conducted our study in eastern Pennsylvania, southeast of Hawk Mountain Sanctuary, in Berks and Lehigh Counties. The 1000-km^2 study area was dominated by agricultural land use and was interspersed with fencerows, woodlots, and riparian forests. Forested areas varied from early-successional to mature stands (>30 yr old) of harvestable timber. Natural vegetation was Appalachian oak (*Quercus* spp.) and oak-hickory (*Carya* spp.)-pine (*Pinus* spp.) associations (Kuchler 1964). Predominant agricultural species were corn (*Maze* spp.), soybeans (*Glycine max*), wheat (*Triticum* spp.), alfalfa (*Medicago* spp.), and mixed grasses (*Lolium* spp., *Festuca* spp., *Trifolium* spp., and *Phleum* spp.) for hay production.

Over the past 25 years, personnel from Hawk Mountain Sanctuary Association have installed 149 nest boxes for breeding kestrels throughout the study area (Heintzelman and Nagy 1968). These boxes were placed in suitable habitat based on qualitative information and unpublished records from Hawk Mountain Sanctuary Association. The mean distance between each nest box was 0.8 km. Kestrel territories probably only included one nest box because the average diameter of kestrel breeding territories in eastern North America is 0.5 km (Bowman and Bird 1986, Gard and Bird 1990). We conducted our research at 130 nest boxes that remained in the same locations for at least five breeding seasons (1987–1991). Most boxes were mounted on deciduous trees (N = 127), and three were mounted on utility poles. Height above ground of boxes ranged from 2.0–6.5 m. All nest boxes were constructed of untreated lumber and had the following internal dimensions: depth = 26 cm, width = 24 cm, and height = 33 cm. The entrance hole was 7.6 cm in diameter and was 26 cm above the floor of the box. Nest-box contents from the previous breeding season were removed from each box in February or early March of each year and replaced with 2.5–5.0 cm of wood chips. In addition, throughout the breeding season, a bed of wood chips was maintained inside nest boxes that were not actively used by kestrels.

Nest-box use and nesting success.—We visited nest boxes during incubation, early nestling, and late nestling periods to determine rates of nest-box use and nesting success. We inspected nest boxes twice during the incubation period and once each during the early

nestling and late nestling periods. These visits were kept brief (<10 min) to minimize any observer-related effects on nesting success. During all three time periods, nests and eggs of European Starlings (*Sturnus vulgaris*) were removed and replaced with 2.5–5.0 cm of fresh wood chips. Nest boxes were inspected during the incubation period to determine breeding activity and clutch size. Nest boxes were not considered active until at least one kestrel egg or eggshell fragments was found inside the box. Each active nest box was considered a nesting attempt. We considered each nesting attempt to be an independent observation, as nest-box fidelity (i.e., reuse of nest boxes by the same individuals) was observed to be low (14%) for this kestrel population (Rohrbaugh 1994).

Nestlings were counted during the first 10 days of the nestling period (early-nestling period). We visited boxes again when nestlings were ≥22 days old (late-nestling period) in order to determine numbers of fledglings. Steenhof and Kockert (1982) recommended that nestlings of diurnal raptors be considered successfully fledged when they attain 80% of average age to fledging; this age is 22 days for kestrels.

Nest-box use was defined as the frequency of nest boxes used by breeding kestrels during a given year. For temporal comparisons, nesting success was calculated as the proportion of nesting pairs that successfully fledged at least one offspring during a given breeding season. For comparisons of nesting success with macrohabitat and microhabitat characteristics, nest boxes were categorized based on the number of years they housed a successful pair of breeding kestrels.

Macrohabitat and microhabitat.—We measured five macrohabitat and 14 microhabitat variables at each nest box in June and July of 1990 and 1991 (Table 1). Macrohabitat variables were distances to key ecological and human-related features in the landscape. Microhabitat variables were vegetative and physical characteristics within a 25-m radius of each nest box. Macrohabitat variables were measured in the field using a meter tape if ≤100 m from the nest box. If distances were >100 m, they were measured from 1:24,000 scale USGS topographic maps or 1:40,000 scale aerial photographs taken in 1987. Microhabitat variables were quantified within a 25-m radius (0.20 ha) circular plot centered on the nest tree at each of the 130 nest boxes.

We determined the percent of Anderson Level III and IV land-use types (PELU) within each plot based on 20, 1 × 1 m square grid samples taken at 5-m intervals along two perpendicular transects centered on the nest tree. We classified nest boxes into three categories based on the percent of "open" land-use types associated with each box. Open land-use types included cropland, pastureland, hayland, and herbaceous rangeland. Nest box locations containing ≥65% (≥13 of 20 grid samples) open land-use types were considered to be in open habitat; those with 30–60% (6–12 of 20 grid samples) open land-use types were considered to be in semi-open habitat; and those with ≤25% (≤5 of 20 grid samples) open land-use types were considered to be in dense habitat.

We measured selection-light intensity (SELT) and nestling-light intensity (NELT) inside each nest box. Selection-light intensity was measured from 5 to 11 March prior to "leaf-out," and at time when nest sites are presumably being selected by kestrels (Heintzelman and Nagy 1968, Stokes 1979). Nestling-light intensity was measured following the fledging of offspring (24 July–7 August). Selection- and nestling-light intensities were measured using a photometer (Curley et al. 1987). The photometer consisted of a cadmium-sulfide photoelectric cell (Tandy Corporation, Fort Worth, Texas, Archer Catalog No. 276-1657) attached to an energy meter. The photoelectric cell was placed inside the nest box through the entrance hole. The cell then was attached to a 10-cm tall wooden stand placed inside the nest box. The access door of the nest box was closed, and the light-intensity measurement was read in microamperes (ma) from the energy meter held outside the nest box (Curley et al. 1987). Light-intensity measurements were taken only between 11:00 and 13:00 h on clear

days (≤30% cloud cover) to eliminate bias that may be created due to angle or intensity of the sun.

Statistical design and analyses.—Three levels of nest-box use were identified: unused boxes (used 0 of 5 years), occasionally used (used 1–2 years), and frequently used (used ≥3 years). We classified nest success as (1) low-nesting success (boxes that housed nesting kestrels, but failed to fledge offspring in 5 years), (2) average-nesting success (boxes that were successful 1 or 2 years), and (3) high-nesting success (boxes that were successful ≥3 years).

We compared macrohabitat and microhabitat variables among levels of nest-box use and nesting success using single-classification analyses-of-variance (ANOVA) (Sokal and Rohlf 1981). When necessary, variables were transformed (arcsin, natural log, or square-root) to meet the assumptions of normality and homogeneity of variance. If a variable differed significantly ($P \leq 0.05$) between levels, we used Student-Newman-Keuls multiple comparison tests to determine locations of the statistical differences (Sokal and Rohlf 1969).

We performed chi-square tests on categorical data using the same levels (categories) of nest-box use and nesting success as with continuous variables. The data were formatted into multi-way contingency tables, and tables with ≥20% of expected counts ≤5, or ≥1 expected count <1 were considered invalid. When a variable was found to be significant ($P \leq 0.05$), the table was collapsed to isolate the cell(s) of interest. These cells then were tested a posteriori using Chi-square tests-of-independence (Sokal and Rohlf 1981).

RESULTS

Nest-box use and nesting success.—Kestrels used 99 (76%) of 130 nest boxes during the 5-year period. The average number of nest boxes used per year was 52 (40%) (range = 35–67, SE = 5.14) (Table 2). There were 31 (24%) unused boxes, 52 (40%) occasionally used (used 1–2 years) boxes, and 47 (36%) frequently used (used ≥3 years) boxes. The mean number of years that a given nest box was used was 2.0 (N = 130, range = 0–5, SE = 0.14). The frequency of nest boxes used differed significantly among years ($\chi^2 = 17.1$, df = 4, $P < 0.005$). The number of nest boxes used during 1987 (N = 67) was significantly higher, and the number used during 1990 (N = 35) was significantly lower than the expected values for those years. In addition, the number of nest boxes used declined annually by an average of 19% from 1987–1990 and then increased by 57% in 1991 (Table 2).

We noted 259 nesting attempts during the five nesting seasons. The mean number of successful nests per year was 25 (49%) (range = 20–28, SE = 1.53) (Table 2). The mean proportion of nests that survived through the incubation period (1987–1991) was 30%. Of the 99 boxes used at least once during the five years, 29 (29%) never fledged young, 57 (58%) fledged young during one or two years, and 13 (13%) fledged young during at least three years. The mean number of years in which a nest box was successful was 1.3 (N = 99, range = 0–4, SE = 0.12).

Macrohabitat.—One (20%) macrohabitat variable differed significantly ($P \leq 0.05$) among levels of nest-box use. Distance to forest (DFOR) was

TABLE 1

MACROHABITAT AND MICROHABITAT VARIABLES MEASURED AT 130 NEST BOXES OF AMERICAN KESTRELS IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1990–91

Variable	Description
Macrohabitat:	
Distance to human habitation (DHUM)	Distance (m) of nest box to nearest building as measured in the field or from topographic maps.
Distance to forest (DFOR)	Distance (m) of nest box to nearest forested area ≥0.5 ha as measured in the field or from aerial photographs.
Distance to active nest box (DBOX)	Mean distance (m) (1987–1991) of nest box to nearest active nest box as measured from topographic maps.
Distance to water (DWAT)	Distance (m) of nest box to nearest body of water, such as a creek, pond, or lake as measured in the field or from topographic maps.
Type of water (TWAT)	Type of closest water (intermittent stream, tributary stream, creek or river, pond or lake) as classified in the field or from topographic maps.
Microhabitat:	
Nest tree dbh (TDBH)	Diameter breast height (cm) of nest tree.
Nest tree health (NTHL)	Estimated health of nest tree based on categorized drawings of trees (Devereux and Mosher 1984).
Nest-box height (NBHT)	Height (m) from bottom of nest box to ground, measured with tape measure.
Nest-box concealment (NBCO)	Percent (%) of nest box concealed by vegetation, measured using a 30- × 380-cm visibility board (Curley et al. 1987).
Nest-box orientation (NBOR)	Compass azimuth in degrees of the entrance hole of the nest box (Balgooyen 1976, 1990, Brauning 1982, Raphael 1985).
Number of suitable perches (PERC)	Number of perches ≥1.5-m tall within the plot (snags, poles, etc.).
Percent land use (PELU)	Percent (%) of each Anderson Level III and IV land use types within each plot based on 20, 1- × 1-m square grid samples at 5-m intervals along two perpendicular transects centered on the nest tree (Anderson et al. 1976).
Shannon-Weiner index (SWIN)	Diversity of Anderson land-use types (levels III and IV) based on the Shannon-Weiner Index (H').

TABLE 1
CONTINUED

Variable	Description
Overstory density (OSHA)	Density (no. stems/ha) of overstory stems (≥10.5-cm dbh).
Understory density (USHA)	Density (no. stems/ha) of woody understory stems (2.5- to 10.5-cm dbh and <1.5-m tall) based on two, 1- × 50-m transects.
Tall shrub density (TSHA)	Density (no. stems/ha) of woody stems 1.5-m tall and <2.5-cm dbh based on two, 1- × 50-m transects.
Short shrub density (SSHA)	Density (no. stems/ha) of woody stems 0.5- to 1.5-m tall and <2.5-cm dbh based on two, 1- × 50-m transects.

TABLE 2

YEAR, NUMBER NEST BOXES USED, PERCENT NEST BOXES USED, AND PERCENT NESTING SUCCESS AT 130 AMERICAN KESTREL NEST BOXES IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1987–91

Year	Number of boxes used	Percent of boxes used	Percent of nesting success
1987	67	52	42
1988	53	41	43
1989	49	38	51
1990	35	27	57
1991	55	42	51
Mean	52	40	49

greater ($P = 0.05$) for occasionally and frequently used nest boxes than for unused nest boxes (Table 3).

Microhabitat.—Nine (64%) microhabitat variables differed significantly ($P \leq 0.05$) among levels of nest-box use and nesting success: nest-box concealment (NBCO), overstory stems/ha (OSHA), understory stems/ha (USHA), tall shrubs/ha (TSHA), short shrubs/ha (SSHA), percent land use (PELU), nest-box orientation (NBOR), selection-light intensity (SELT), and nestling-light intensity (NELT).

Nest-box concealment, which was highly correlated with nestling-light intensity ($r = -0.47$, df = 106, $P < 0.05$), differed ($P = 0.05$) among levels of nest-box use, with frequently used nest boxes having the lowest percent concealment (Table 3).

Density of overstory stems ($P = 0.00$), understory stems ($P = 0.00$), tall shrubs ($P = 0.00$), and short shrubs ($P = 0.04$) differed among levels of nest-box use (Table 3). However, these variables were highly correlated ($P \leq 0.05$) with each other. Results from percent land use (PELU) measures indicated that kestrels most frequently used nest boxes associated with open habitats dominated by herbaceous vegetation ($\chi^2 = 16.8$, df = 4, $P < 0.005$) (Fig. 1). These open habitats frequently were bottomland pastures that lacked vertical structure.

Nest-box orientation differed among levels of nest-box use ($\chi^2 = 14.6$, df = 6, $P < 0.025$). Kestrels used nest boxes oriented southeast more frequently than expected ($\chi^2 = 13.35$, df = 2, $P < 0.005$) and avoided northwestern facing boxes ($\chi^2 = 6.2$, df = 2, $P < 0.05$). Boxes in all other orientations were used in proportion to their availability (Fig. 2). Twenty-six (90%) of 29 nest boxes oriented southeast were used at least one year during the 5-year period, and 18 (62%) were used ≥3 years.

TABLE 3

F-RATIOS, *P*-VALUES, AND MEANS (SE) OF EIGHT VARIABLES[a] MEASURED AT 130 AMERICAN KESTREL NEST BOXES IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1990–91

				Mean (SE) for nest-box use levels		
Variable	Transformation	F	P	Unused	Occasionally used	Frequently used
NELT	UT[b]	4.11	0.018	5.09 (0.37)	5.86 (0.27)	6.39 (0.27)
NBCO[a]	UT	2.94	0.056	46.32 (6.32)	40.00 (4.97)	28.13 (4.59)
NBCO	AS[c]	3.02	0.052	0.58 (0.10)	0.48 (0.07)	0.32 (0.06)
OSHA	UT	8.52	0.000	67.32 (13.75)	29.67 (4.76)	23.81 (5.19)
USHA	UT	11.36	0.000	112.52 (23.50)	32.63 (7.60)	22.11 (11.76)
TSHA	UT	7.60	0.001	590.32 (182.89)	188.46 (48.09)	106.38 (33.92)
SSHA	UT	1.74	0.180	1435.16 (369.77)	726.92 (149.71)	1014.87 (280.59)
SSHA	LN[d]	3.18	0.045	5.26 (0.63)	3.15 (0.53)	3.48 (0.57)
DFOR	UT	3.03	0.052	221.93 (26.35)	390.68 (51.84)	343.39 (40.77)

[a] The variables were tested using ANOVA to examine differences among levels of nest-box use. Descriptions of variable acronyms are given in Table 1.
[b] Variable untransformed for final analyses.
[c] Variable transformed using arcsin for final analyses.
[d] Variable transformed using natural log for final analyses.

Furthermore, 36 (77%) of the 47 frequently used nest boxes faced eastward (0–180°).

Means for selection-light intensity and nestling-light intensity were 6.7 ma (range = 3.5–9.5, SE = 0.11) and 5.9 ma (range = 1.0–9.3, SE = 0.17), respectively. We did not observe a significant difference in selection-light intensity (F = 1.19; df = 2, 121; P = 0.31) among levels of nest-box use. However, selection-light intensity was significantly higher in the high nesting success level versus the low or average levels (F = 3.15; df = 2, 121; P = 0.047). Mean selection-light intensities were 6.66 (0.23), 6.67 (0.15), and 7.57 ma in the low, average, and high nesting success levels, respectively. Nestling-light intensity differed (P = 0.018) among levels of nest-box use, and was highest at frequently used boxes (Table 3).

DISCUSSION

Nesting success.—The mean rate of nesting success for kestrels in our study (49%) was intermediate to success rates observed elsewhere: Ken-

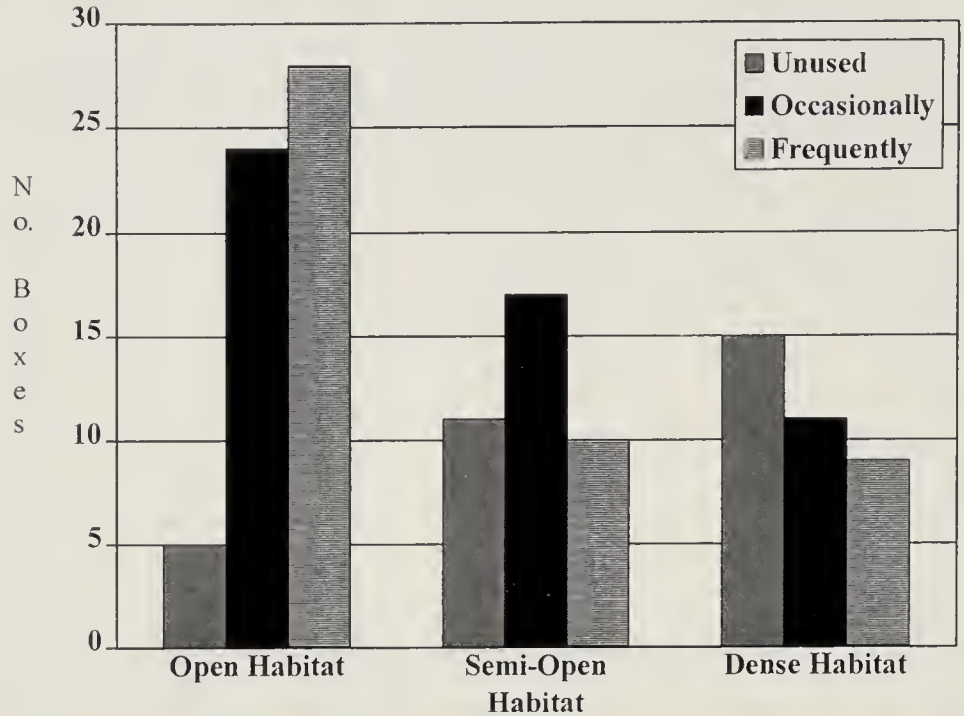

FIG. 1. Number of unused, occasionally used (used 1–2 of 5 years), and frequently used (used ≥3 of 5 years) American Kestrel nest boxes associated with open, semi-open, and dense habitats in Berks and Lehigh counties, Pennsylvania.

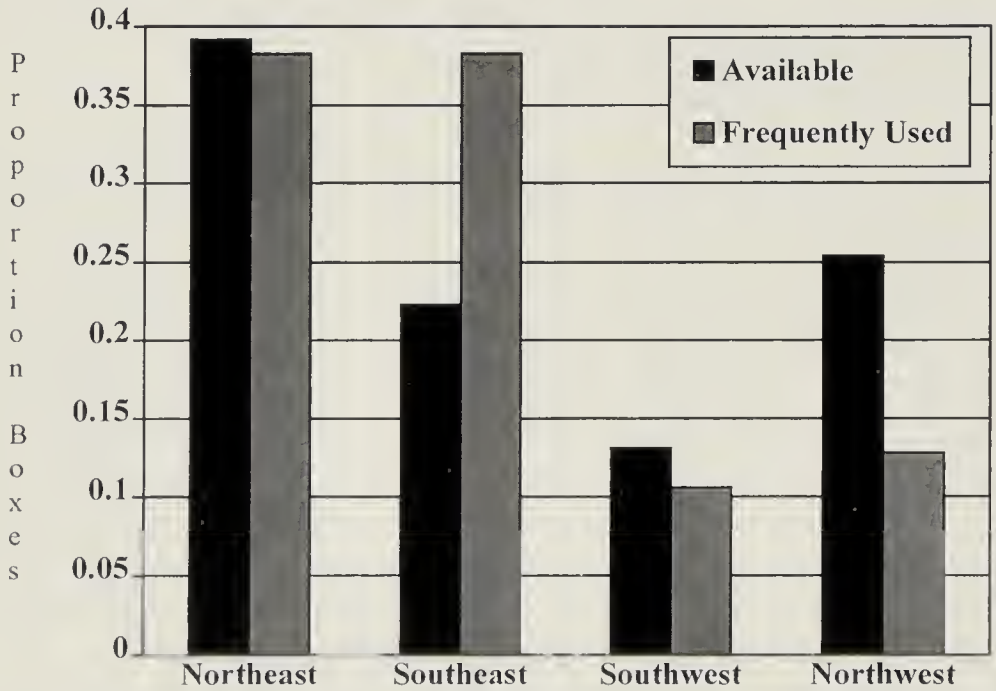

FIG. 2. Proportionate distributions of 130 nest boxes available for use by American Kestrels and 47 nest boxes that were frequently used (used ≥3 of 5 years) by kestrels within four compass azimuth orientations in Berks and Lehigh counties, Pennsylvania.

tucky—36% (Kellner and Ritchison 1988), Wisconsin—67% (Hamerstrom et al. 1973), Idaho—81% (Craig and Trost 1979), California—82% (Bloom and Hawks 1983), and Missouri—86% (Toland and Elder 1987). Apanius (1992) observed similar nesting success (44%) by kestrels in our study area. The low-to-intermediate rate of nesting success exhibited by kestrels in our study may have been a result of nest desertion during the incubation period, as 70% of nest failures occurred during this period. Subsequent to the commencement of incubation in early May, the habitat of the study area was altered extensively by agricultural practices (e.g., plowing, planting, and spraying, of agricultural fields). These habitat alterations and disturbances may influence rates of nest desertion in kestrels.

In recent years, mechanized farming coupled with the use of modern fertilizers and pesticides (i.e., herbicides and insecticides) have enabled farmers to harvest hay and grain crops earlier and more frequently (Castrale 1985, Best 1986, Rodenhouse et al. 1993, Warner 1994). Earlier and more frequent harvests may reduce diversity and biomass of prey species (i.e., insects and small vertebrates; Bollinger et al. 1990, Frawley and Best 1991, Gard et al. 1993). In our study area, some harvests are coincident with the latter stages of incubation in late May and early June. In addition, the rapid conversion of dormant agricultural fields to row crops in spring may substantially reduce prey availability and abundance during the incubation period. Moreover, land-use changes (i.e., residential and commercial development) have reduced the amount of alternate hunting habitats for kestrels. Although not documented in American Kestrels, nest desertion during the incubation period associated with low prey availability is the most prominent cause of nest failures in Eurasian Kestrels (*Falco tinnunculus*) (Village 1990).

Inter-specific competition.—In North America, starlings are frequently associated with agricultural and human-dominated landscapes. Starlings usurp nest boxes during the kestrel egg-laying stage, often causing kestrels to abandon a partial clutch of eggs before incubation commences (Hamerstrom et al. 1973, Wilmers 1987). In our study, eggs of usurped kestrel nests often were punctured, and starling nests were constructed on top of the kestrel eggs. Puncturing of kestrel eggs by starlings has not been documented, but starlings are known to puncture eggs of Wood Ducks (*Aix sponsa*) (Bellrose et al. 1964, Muncy and Burbank 1975). Starlings may have precluded the use of nest boxes and reduced nesting success of kestrels. We have accurate data on the use of nest boxes by starlings for the final year (1991) of our study. During this year, starlings used 57 (42%) nest boxes, and 17 (30%) of these also were used by kestrels at some time during the breeding season. Eleven (65%) of the 17 nesting attempts initiated by kestrels in boxes occupied by starlings were

unsuccessful, whereas only 14 (37%) of 38 nesting attempts by kestrels in boxes unoccupied by starlings were unsuccessful.

Other nest-box competitors include, gray squirrels (*Sciurus carolinensis*) and white-footed mice (*Peromyscus leucopus*). Nest boxes situated <150 m from forested areas were often used by these two species. This may partially explain why occasionally and frequently used nest boxes were on average situated 145 m farther from forested areas than unused boxes.

Microhabitat relationships.—Curley et al. (1987) found that kestrels selected nest boxes with high-light intensities inside the box. Richards (1970) and Wilmers (1987) suggested that this preference for high-light environments was a consequence of recent evolutionary changes in nesting behavior of kestrels. Richards (1970) proposed that cavity nesting by kestrels was a relatively recent occurrence, which evolved subsequent to the use of open nests. Eggs of kestrels are heavily marked, unlike the pale eggs of most cavity-nesting birds, suggesting that kestrels evolved in high-light environments (i.e., open nests). Our observation that nest-box use increased with greater nestling-light intensity was perhaps a consequence of the amount of nest-box concealment and not differences in nestling-light intensity per se. Kestrels probably used nest boxes with high nestling-light intensities more frequently because these boxes also had low nest-box concealment.

Nest boxes with low concealment may attract kestrels because they are more visible than those with high concealment or because low nest-box concealment allows an unobstructed flight path into the box. An unobstructed flight path into the nest box may be important when kestrels deliver prey to mates and nestlings. Curley et al. (1987) reported that starlings have a preference for nest boxes with high nest-box concealment and low-interior light intensity. Hence, usurpation of kestrel nest boxes by starlings may be less frequent at boxes with low concealment and high nestling-light intensity. However, for the one year that we have starling data (1991), we found no relationship between use of nest boxes by starlings and nestling-light intensity ($F = 1.1$; df = 1, 125; $P = 0.30$).

We confirmed that kestrels have a preference for nest boxes (cavities) that are oriented southeast, which was similar to results obtained by Brauning (1982). He noted that these southeast-facing nests averaged higher morning temperatures and lower afternoon temperatures than cavities oriented in other directions. Balgooyen (1976, 1990) suggested that cavities facing eastward provide thermoregulatory advantages because of warmth of morning sun and protection from hot afternoon temperatures, thereby reducing thermoregulatory stress and theoretically increasing nesting success. We found that nesting success of kestrels using boxes

oriented southeast or eastward did not differ from nesting success of kestrels using boxes with other orientations. However, high nest-box concealment may nullify the thermoregulatory effects of orientation by blocking sunlight, and this may explain why kestrels nesting in boxes with high selection-light intensity exhibited increased nesting success in our study. Increased selection-light intensity may result in higher temperatures and lower moisture inside the nest box during early morning and evening, which may be important during incubation when ambient temperatures are relatively low.

We noted that kestrels most frequently used boxes located in extremely open habitats dominated by herbaceous vegetation. Smallwood and Collopy (1991) noted a similar relationship between nest-box use and openness of habitat at 355 nest boxes erected in hardwood hammocks and longleaf pine (*Pinus palustris*)-turkey oak (*Quercus catesbaei*) sandhills in north-central Florida. Occupancy rates of nest boxes located in the more open sandhills were twice that of boxes located in hammocks, and percent nesting success was greater in sandhills (67%) than in hammocks (36%).

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BREEDING BIRD COMMUNITIES AND NEST PLANT SELECTION IN CHIHUAHUAN DESERT HABITATS IN SOUTH-CENTRAL NEW MEXICO

JEFFREY M. KOZMA[1] AND NANCY E. MATHEWS[1,2]

ABSTRACT.—We examined the significance of arroyo-riparian habitat to birds in the Chihuahuan Desert of south-central New Mexico. Nests (N = 620) of 27 species were monitored during 1993–1995. Twenty-three species nested in arroyos and 20 species nested in uplands. Northern Mockingbirds (*Mimus polyglottos*), Rock Wrens (*Salpinctes obsoletus*), and Verdins (*Auriparus flaviceps*) nested most frequently in arroyos. Black-throated Sparrows (*Amphispiza bilineata*), Northern Mockingbirds, and Scott's Orioles (*Icterus parisorum*) nested most frequently in uplands. Nest density in arroyos was more than twice that of uplands (0.64 nests/ha versus 0.27 nests/ha). Nest success and predation rates did not differ between arroyos and uplands for Black-throated Sparrows, Northern Mockingbirds, and Crissal Thrashers (*Toxostoma crissale*). Nest predation was the primary cause of mortality to eggs and nestlings in both habitats. Torrey yucca (*Yucca torreyi*), javelina bush (*Condalia warnockii*), and little-leaf sumac (*Rhus microphylla*) were the most frequently used nest substrates, even though these shrubs were among the lowest in density. Maintaining this habitat and protecting sparse shrub species used as nest substrates may have long term importance in managing Chihuahuan Desert bird communities. *Received June 23, 1996, accepted December 5, 1996.*

Populations of some Neotropical migrants have declined over the last 20–30 years (Finch 1991). A significant reason for these declines is thought to be caused by loss of habitat on both breeding and wintering grounds (Wilcove and Whitcomb 1983, Robbins et al. 1989). In order to conserve populations of Neotropical migrants, as well as resident species, it is necessary to understand not only their habitat requirements, but their demographic patterns as well (Martin 1992). Such understanding may provide insight into the evolutionary and ecological factors that influence their fitness (Martin and Geupel 1993). However, for some species in North America, little information exists about basic habitat requirements, reproduction, and survival (Martin 1993, Martin and Geupel 1993).

In this study, we focus on several questions to expand the understanding of ecological factors influencing populations of Neotropical migrants and resident birds in arroyo-riparian and surrounding upland habitat in the Chihuahuan Desert. We hypothesize that breeding bird richness and nesting success is higher in arroyo habitat than in the xeric upland habitat and that birds show disproportionate use of all nesting species of shrubs.

[1] U.S. National Biological Service, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech Univ., Lubbock, Texas, 79409-2125.
[2] Present address: 7500 Westbrook Ct., Yakima, Washington 98908.

Our objectives were (1) to determine the composition of the breeding bird communities in both arroyo and upland habitat; (2) to compare nesting success in both habitats and (3) to evaluate nesting plant preferences and life history information.

METHODS

Study site.—Our study area is located 22 km northeast of Orogrande, Otero Co., New Mexico, on the McGregor Range, on the Fort Bliss Military Reservation. The main portion of Fort Bliss rests in the Tularosa Basin surrounded by the San Andres, Franklin and Organ mountains on the west and the Sacramento and Hueco mountains on the east. Elevation of the site ranges from 1276 m to 1512 m. Rainfall averages between 20.3 to 25.4 cm annually (Budd et al. 1979). Approximately 65% to 80% of the annual rainfall occurs from June to September (Shreve 1942). The predominant arroyo vegetation is little-leaf sumac (*Rhus microphylla*), desert willow (*Chilopsis linearis*), apache plume (*Fallugia paradoxa*), and brickell bush (*Brickellia laciniata*). Arroyos are classified here as riparian habitat since they contain plant associations different from those of the adjacent upland, even though they may not contain flowing water for many years (Ohmart and Anderson 1986). The vegetation in adjacent uplands is desert scrub (Shreve 1942) or bajada. Dominant shrubs include whitethorn acacia (*Acacia constricta*), mesquite (*Prosopis glandulosa*), creosote bush (*Larrea tridentata*), and tarbush (*Flourensia cernua*). Torrey yucca (*Yucca torreyi*), soaptree yucca (*Y. elata*), and banana yucca (*Y. baccata*) are found in clumps throughout the uplands. Grasses and forbs throughout the area are dominated by *Aristida* spp., black grama (*Bouteloua eriopoda*), bush muhly (*Muhlenbergia porteri*), broom snakeweed (*Guterrezia sarothrae*), and Gordon's bladderpod (*Lesquerella gordoni*).

We chose eight arroyos for our study plots based on the presence of (1) a well-defined gravel channel, (2) obligate arroyo plants (i.e., apache plume and brickell bush), (3) a band of arroyo vegetation that averaged between 30–50 m wide and at least 1400 m in length, and (4) compatibility with proposed military activities and access. We chose adjacent uplands for comparison (on one side of the arroyo) based on the lack of intersections with other major arroyos and continuity of cover within a 44.8 ha area. The sample plots were 56 ha (1400 × 400 m) and consisted of a combination of arroyo and upland, of which arroyo habitat comprised approximately 20% (11.2 ha; 1400 × 80 m).

Nest searching.—We began nest searching the first week of May in 1993, 1994 and 1995. We found nests by following adults carrying nesting material or food, flushing adults from nests, and actively searching for nests in possible nesting sites (i.e., large yuccas). We proportioned time spent nest searching equally between habitats and visited plots every other day to ensure that nesting cycles and causes of nest failure were documented accurately. When checking a nest, we recorded which adults, if any, were present, nest contents (e.g., number of eggs/young, cowbird eggs), and fate of nest (e.g., fledged, abandoned, depredated, failure due to weather, and other). If no adults were observed for five or more consecutive checks and the contents of the nest remained unchanged, we assigned a fate of deserted. If all eggs or young were gone before the anticipated time of incubation or nestling stage was complete, we assigned a fate of depredated.

Vegetation sampling.—We sampled vegetation at a total of 256 points in each habitat, following guidelines proposed by James and Shugart (1970). Points were selected systematically with a 5-m radius circle centered on each point. Within this circle, we counted all shrubs and yuccas. We also used five, 1 m diameter circles around each point and counted the number of forbs (e.g., broom snakeweed) and grasses rooted in the circle.

Analysis.—We calculated nest success for those species with ten or more nests per habitat,

using the modified Mayfield Method (Mayfield 1975, Hensler and Nichols 1981) and the program Micromort (Heisey and Fuller 1985). A nest was considered successful if one or more young fledged. We used ANOVA to compare nest densities between habitats and *t*-tests to compare clutch sizes and mean numbers of young fledged between habitats. We used the program Contrast (Sauer and Williams 1989), which utilizes a modified Chi-square statistic, to compare survival and predation rates between arroyos and uplands for species with at least ten nests in each habitat. We used Kendall's coefficient of rank correlation (Sokal and Rohlf 1981) to rank correlate numbers of nests with densities of shrub species used in both habitats. We also used Kendall's coefficient of rank correlation to rank correlate numbers of Black-throated Sparrow and Northern Mockingbird nests with densities of shrub species used. These two species were the only species to have adequate sample sizes to perform rank correlation analyses. All analyses were performed at $\alpha \leq 0.05$.

RESULTS

We found a total of 620 nests of 27 species during 1993–1995 (Table 1). Of these 27 species, 16 were non-migratory (59.3%), nine were neotropical migrants (33.3%), and two were short distance migrants (7.4%) (Finch 1991). Of all non-migratory species, 37% nested most frequently in arroyos, 37% nested most frequently in uplands, and 25% nested about equally in both habitats. Six of nine Neotropical migrant species (66.7%) and both short distance migrant species nested more frequently in uplands.

Twenty-three species nested in arroyos and 20 species nested in uplands (Table 1). Northern Mockingbirds, Rock Wrens, Verdins, and Crissal Thrashers were the most frequently nesting species in arroyos. Black-throated Sparrows, Northern Mockingbirds, Scott's Orioles, and House Finches were the most frequently nesting species in uplands. Nest density in arroyos (0.64 nests/ha) was significantly greater than in uplands (0.27 nests/ha) ($P = 0.002$). Peak nest initiation of all species combined, occurred between 18 and 24 May in each year.

In arroyos, Black-chinned Hummingbirds achieved the greatest nest success of the five species with sample sizes adequate for analysis (Table 2). For four species, predation accounted for the greatest loss of nests; for Canyon Towhees abandonment accounted for the greatest losses. In uplands, Northern Mockingbirds achieved the highest nest success of the eight species with sample sizes adequate for analysis (Table 2). Again, predation accounted for the greatest loss of nests. Nest success and predation rates did not differ between arroyos and uplands for Black-throated Sparrows ($\chi^2 = 2.621$, 1 df, $P = 0.106$ and $\chi^2 = 1.481$, 1 df, $P = 0.224$, respectively), Northern Mockingbirds ($\chi^2 = 0.261$, 1 df, $P = 0.610$ and $\chi^2 = 0.268$, 1 df, $P = 0.605$, respectively), and Crissal Thrashers ($\chi^2 = 1.126$, 1 df, $P = 0.289$ and $\chi^2 = 0.718$, 1 df, $P = 0.397$). These three species were the only ones with sample sizes large enough to compare between habitats, although the scale and proximity of these habitats make comparing productivity difficult. We believe snakes were the primary nest

TABLE 1

TOTAL NUMBER OF NESTS FOUND FOR ALL SPECIES, BY HABITAT, ON THE MCGREGOR RANGE, FORT BLISS, TEXAS IN 1993–1995

Species	Total	Arroyo	Upland
Black-throated Sparrow (*Amphispiza bilineata*)[a]	141	12	129
Northern Mockingbird (*Mimus polyglottos*)[b]	113	31	82
Scott's Oriole (*Icterus parisorum*)[c]	48	2	46
House Finch (*Carpodacus mexicanus*)[a]	35	9	26
Crissal Thrasher (*Toxostoma crissale*)[a]	33	17	16
Verdin (*Auriparus flaviceps*)[a]	31	19	12
Loggerhead Shrike (*Lanius ludovicianus*)[a]	28	7	21
Rock Wren (*Salpinctes obsoletus*)[a]	23	22	1
Western Kingbird (*Tyrannus verticalis*)[c]	23	1	22
Canyon Towhee (*Pipilo fuscus*)[a]	19	12	7
Ash-throated Flycatcher (*Myiarchus cinerascens*)[c]	18	9	9
Common Nighthawk (*Chordeiles minor*)[c]	16	0	16
Cactus Wren (*Campylorhynchus brunneicapillus*)[a]	15	8	7
Mourning Dove (*Zenaida macroura*)[a]	14	0	14
Black-chinned Hummingbird (*Archilochus alexandri*)[c]	10	10	0
Black-tailed Gnatcatcher (*Polioptila melanura*)[a]	10	2	8
Blue Grosbeak (*Guiraca caerulea*)[c]	8	8	0
Common Poorwill (*Phalaenoptilus nuttallii*)[c]	8	0	8
American Kestrel (*Falco sparverius*)[a]	5	5	0
Greater Roadrunner (*Geococcyx californianus*)[a]	5	5	0
Say's Phoebe (*Sayornis saya*)[c]	5	3	2
Phainopepla (*Phainopepla nitens*)[b]	4	1	3
Lesser Nighthawk (*Chordeiles acutipennis*)[c]	3	0	3
Rufous-crowned Sparrow (*Aimophila ruficeps*)[a]	2	1	1
Barn Owl (*Tyto alba*)[a]	1	1	0
Ladder-backed Woodpecker (*Picoides scalaris*)[a]	1	1	0
Pyrrhuloxia (*Cardinalis sinuatus*)[a]	1	1	0
Total number of nests	620	188	432

[a] Non-migrant (year-round resident)

[b] Short-distance migrant (absent from the study area during some part of the year, but winters primarily within the United States).

[c] Neotropical migrant (winters in the tropical and sub-tropical latitudes of Central and South America and whose main wintering areas are south of the United States).

predators on all nests, as indicated by the lack of disturbance at the nest site, although some avian species (i.e., Greater Roadrunners) are known to prey on nests and leave little evidence of disturbance. However, avian predators were rare on our sites and for other predators we were unable to collect detailed information on their populations.

Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was a source of nest failure for four species. Black-tailed Gnatcatcher (*Polioptila melanura*) nests were the most heavily parasitized of all species; 50%

TABLE 2

PERCENT NEST SUCCESS AND MORTALITY FACTORS FOR TEN[a] NESTING SPECIES IN ARROYO AND UPLAND HABITAT ON THE FORT BLISS MILITARY RESERVATION, FORT BLISS, TEXAS, IN 1993–1995

Species	N	Exposure[b]	Survival[c]	Predation	Abandoned	Other	Weather	Parasitism
				Arroyo				
Northern Mockingbird	31	481	0.50 (0.10)	0.42 (0.10)	0.08 (0.07)	0.0	0.0	0.0
Crissal Thrasher	16	274.5	0.29 (0.10)	0.53 (0.12)	0.12 (0.08)	0.06 (0.06)	0.0	0.0
Canyon Towhee	14	109	0.19 (0.11)	0.30 (0.14)	0.40 (0.15)	0.0	0.0	0.10 (0.10)
Black-throated Sparrow	12	113	0.13 (0.09)	0.77 (0.12)	0.0	0.10 (0.09)	0.0	0.0
Black-chinned Hummingbird	9	253.5	0.65 (0.16)	0.23 (0.14)	0.12 (0.11)	0.0	0.0	0.0
				Upland				
Black-throated Sparrow	123	1393.5	0.29 (0.04)	0.61 (0.05)	0.05 (0.02)	0.01 (0.01)	0.0	0.03 (0.02)
Northern Mockingbird	80	1332	0.56 (0.06)	0.36 (0.06)	0.08 (0.03)	0.0	0.0	0.0
Scott's Oriole	44	851	0.47 (0.08)	0.34 (0.07)	0.15 (0.05)	0.0	0.05 (0.11)	0.0
House Finch	26	321.5	0.20 (0.08)	0.60 (0.11)	0.20 (0.09)	0.0	0.0	0.0
Loggerhead Shrike	21	384.5	0.39 (0.12)	0.54 (0.13)	0.07 (0.07)	0.0	0.0	0.0
Western Kingbird	21	549.5	0.47 (0.11)	0.43 (0.11)	0.10 (0.06)	0.0	0.0	0.0
Crissal Thrasher	15	258	0.47 (0.13)	0.38 (0.13)	0.15 (0.10)	0.0	0.0	0.0
Mourning Dove	13	151	0.15 (0.09)	0.76 (0.11)	0.08 (0.08)	0.0	0.0	0.0

[a] Containing enough nests with adequate exposure days to calculate nest success.
[b] Total number of exposure days.
[c] Percent of nests that fledged at least one young. Numbers in parentheses represents standard error.

of the nests we located contained at least one cowbird egg. In contrast, only 14% of Blue Grosbeak nests, 10% of Black-throated Sparrow nests, and 5% of Canyon Towhee nests were parasitized. All gnatcatcher nests that were parasitized (N = 5) failed to produce young. Each of the species parasitized accepted Brown-headed Cowbird eggs, with the exception of desertion at one Canyon Towhee nest and one gnatcatcher nest.

Of the ten most abundant nesting species in both habitats, only one species produced significantly different clutch sizes between arroyos and uplands. Black-throated Sparrows produced a higher mean clutch size ($P = 0.02$) and tended to fledge a greater number of young in uplands ($P = 0.190$) (Table 3). Mean clutch sizes and mean number of young fledged for the other nine species did not differ between habitats. Mourning Doves had the smallest average clutch size and thus fledged the fewest young (Table 3).

Little-leaf sumac and mesquite were used for nesting by the greatest number of bird species, followed by Torrey yucca and javelina bush (Table 4). Torrey yucca, javelina bush, little-leaf sumac, and walls of arroyos were the most frequently used nest substrates of the 26 confirmed nesting species in both arroyo and upland habitats (Table 4). Kendall's coefficient of rank correlation analysis did not reveal a significant correlation between the number of nests placed in a particular shrub species and the abundance of that shrub (Table 5) in either habitat for all bird species combined (tau = −0.0545 and tau = −0.110, in arroyos and uplands respectively).

Nest plant selection appears to be different between Black-throated Sparrows and Northern Mockingbirds. Kendall's coefficient of rank correlation did not reveal a significant correlation between number of sparrow nests placed in a particular shrub species and the abundance of that shrub in uplands (tau = 0.2946). Similarly, mockingbirds showed no preference for a particular shrub species in arroyos (tau = −0.4243). However, Kendall's coefficient did reveal a significant negative correlation for mockingbird nests placed in a particular shrub species and the abundance of that shrub in uplands (tau = −0.740).

DISCUSSION

Nesting bird species richness on our study area was greater than in previous studies investigating nesting bird communities of Chihuahuan Desert wash and scrub habitat (Raitt and Maze 1968, Naranjo and Raitt 1993). Raitt and Maze (1968) found eight breeding species in a predominately creosote bush upland dissected with arroyos. Similarly, Naranjo and Raitt (1993) found 11 breeding species in three habitats along a bajada that contained a large creosote/grassland component. However, spe-

TABLE 3

NEST PRODUCTIVITY DATA FOR THE 10 MOST ABUNDANT NESTING SPECIES, BY HABITAT, ON THE MCGREGOR RANGE, FORT BLISS, TEXAS, IN 1993–1995

	Arroyo				Upland			
	Observed slutch size		Number of young fledged		Observed clutch size		Number of young fledged	
Species[b]	Mean	SE[a]	Mean	SE	Mean	SE	Mean	SE
Black-throated Sparrow	2.27[c] (11)[d]	0.19	0.58 (12)	0.31	2.79 (99)	0.07	1.11 (121)	0.12
Northern Mockingbird	3.39 (28)	0.13	1.54 (28)	0.27	3.51 (71)	0.08	1.80 (80)	0.16
Scott's Oriole	4.00 (1)	—	2.00 (2)	2.00	3.76 (38)	0.19	1.59 (41)	0.27
Crissal Thrasher	2.60 (15)	0.16	0.76 (17)	0.30	2.85 (14)	0.09	0.93 (15)	0.26
House Finch	3.20 (5)	0.37	1.16 (6)	0.60	3.94 (17)	0.18	1.07 (26)	0.31
Loggerhead Shrike	4.67 (6)	0.21	2.85 (7)	0.74	4.93 (15)	0.37	2.33 (21)	0.51
Western Kingbird	—	—	—	—	4.22 (18)	0.15	1.57 (21)	0.40
Canyon Towhee	3.29 (7)	0.18	1.58 (12)	0.48	3.00 (4)	0.58	1.29 (7)	0.52
Mourning Dove	—	—	—	—	1.92 (13)	0.08	0.46 (13)	0.24
Black-chinned Hummingbird	2.00 (9)	0.0	1.00 (10)	0.30	—	—	—	—

[a] Standard error.
[b] Rank determined by total number of nests in both habitats combined.
[c] Significantly different between habitats at ≤ 0.05.
[d] Number of nests where clutch size and number of young fledged were determined.

TABLE 4

THE FREQUENCY OF NEST PLANTS AND OTHER SUBSTRATES BY NESTING BIRDS IN BOTH HABITATS ON THE MCGREGOR RANGE, FORT BLISS, TEXAS, IN 1993–1995

Nest substrate	Total nests	Arroyo	Upland	Number of species[a]
Torrey yucca (*Yucca torreyi*)	109	4	105	9
Javelina bush (*Condalia warnockii*)	103	13	90	9
Little-leaf sumac (*Rhus microphylla*)	61	55	6	11
Arroyo wall	39	34	5	5
White-thorn acacia (*Acacia constricta*)	29	9	20	7
Algerita (*Berberis trifoliata*)	24	5	19	6
Ephedra sp.	24	1	23	5
Mesquite (*Prosopis glandulosa*)	24	15	9	11
Soaptree yucca (*Y. elata*)	22	4	18	5
Cholla cactus (*Opuntia imbricata*)	20	9	11	5
Allthorn (*Koeberlinia spinosa*)	19	3	16	7
Broom snakeweed (*Gutierrezia sarothrea*)	16	0	16	2
Creosote bush (*Larrea tridentata*)	16	1	15	3
Desert willow (*Chilopsis linearis*)	14	14	0	7
Grasses[b]	12	1	11	3
Mariola (*Parthenium incanum*)	12	0	12	3
Banana yucca (*Y. baccata*)	11	0	11	3
Tarbush (*Flourensia cernua*)	10	1	9	5
Skeleton-leaf goldeneye (*Viqueria stenoloba*)	9	2	7	4
Apache plume (*Fallugia paradoxa*)	7	7	0	5
Tasajillo (*O. leptocaulis*)	4	0	4	1
Other[c]	35	7	28	10

[a] Includes ground nesting birds that nested within 30 cm of a plant species.
[b] Includes *Aristida* spp., black grama, bush muhly, and plains bristlegrass (*Setaria leucopila*).
[c] Includes plant species with three or fewer nests.

cies richness on our site is significantly lower than in larger, more mesic, riparian habitats in Arizona that contain perennial water and large trees (Carothers et al. 1974, Stamp 1978).

Nesting bird species richness was similar in arroyos and uplands. Rock Wrens, Crissal Thrashers, Northern Mockingbirds, and Verdins were the most frequent nesting species in arroyos. This differs slightly from Raitt and Maze (1968) who found that in southern New Mexico, the most frequently nesting species in arroyos were Verdins and Black-throated Sparrows. Of the 27 confirmed breeding species in our study, nine nested predominantly in arroyos and eight predominantly in uplands. The large number of bird species nesting more frequently in upland habitat is unusual. Raitt and Maze (1968) found that only Black-throated Sparrows and Mourning Doves nested in upland divides between arroyos. However, their study was performed in habitats dominated by creosote bush which

TABLE 5

DENSITY OF THE 15 MOST FREQUENTLY USED NEST PLANT SPECIES IN ARROYO AND UPLAND HABITAT ON THE MCGREGOR MISSILE FIRING RANGE, FORT BLISS, TEXAS IN 1993–1995

	Arroyo		Upland	
Species	Stems/ha	SE	Stems/ha	SE
Broom snakeweed[a]	3826.1	815.43	10,867.4	7452.52
Mariola	6028.5	866.67	6988.3	927.56
Creosote Bush	1477.2	399.08	1818.3	180.16
Tarbush	939.5	259.88	1437.4	181.42
White-thorn acacia	540.1	191.61	1118.6	318.08
Mesquite	124.8	12.63	137.8	60.45
Banana yucca	85.0	72.87	151.7	86.61
Little-leaf sumac	208.9	36.29	6.0	4.32
Mormon tea	47.2	17.04	86.5	25.61
Allthorn	5.0	2.89	5.5	2.81
Algerita	6.0	3.01	1.0	1.00
Javelina bush	2.5	2.49	3.0	1.25
Soaptree yucca	4.5	1.58	0.5	0.50
Torrey yucca	0.8	0.39	1.79	0.62

[a] Rank determined by total stem density across both habitats.

is rarely used by birds for nesting (Anderson and Anderson 1946). In contrast, Naranjo and Raitt (1993) found a greater number of bird species on a Chihuahuan Desert bajada than reported by Raitt and Maze (1968) and attributed this difference to the presence of large mesquite and yuccas on their study area.

We believe that the greater diversity of upland shrubs on our study area may explain the larger number of species found nesting there. Of the eight species nesting predominantly in uplands, four build open-cup nests (Scott's Orioles, Western Kingbirds, Black-tailed Gnatcatchers, and Black-throated Sparrows), and four nest on the ground. Scott's Orioles and Western Kingbirds nested exclusively in large Torrey and soaptree yuccas, both of which reach their highest density and tallest stature in uplands. It is, therefore, not surprising that orioles and kingbirds nest almost exclusively in uplands (Dixon 1959, Naranjo and Raitt 1993). Likewise, gnatcatchers nested in large allthorn shrubs that were more abundant in uplands. Black-throated Sparrows nested within 45.8 cm of the ground, and it is likely that more nesting sites were available to them in uplands due to the greater abundance of small, compact shrubs. Other predominant upland nesting species (Common Nighthawk, Lesser Nighthawk, Common Poorwill, and Mourning Dove built little or no nest and laid their eggs predominantly on bare ground. Their presence was prob-

ably due to sparse ground vegetation (i.e., grasses and forbs) and a lower probability of being swept away by running water during rain storms.

Of the nine species nesting predominantly in arroyos, four were cavity nesters and five were open-cup nesters. Rock Wrens, American Kestrels, and Barn Owls nested in holes in high banks of arroyos; thus suitable upland sites were not available. A single Ladder-backed Woodpecker (*Picoides scalaris*) nest was located in a large desert willow, which was only found in arroyo habitat. The other obligate arroyo nesters (Black-chinned Hummingbird, Blue Grosbeak, Greater Roadrunner, Rufous-crowned Sparrow [*Aimophila ruficeps*], and Pyrrhuloxia [*Cardinalis sinuatus*]) appear to be less nest substrate-specific than exclusive upland nesters. The reasons for their exclusive use of arroyos in this study is not clear, although choice of the greater shrub density and taller stature of shrubs found in arroyo habitat may relate to food resources or protective cover for nesting.

Our finding of greater nest density in arroyo habitat concurs with that of Raitt and Maze (1968) and Tomoff (1974). The presence of more dense and large shrubs, again, may offer greater opportunities for nesting and improved concealment from predators.

Nest success rates for bird species on our study area correspond with those previously reported. Nest success for Northern Mockingbirds in both habitats was similar to success rates previously reported in Tennessee and Florida (Laskey 1962, Joern and Jackson 1983). Black-throated Sparrows achieved nest success rates in uplands similar to those reported by Delesantro (1978) in southern New Mexico. However, nest success for Loggerhead Shrikes in uplands and for Crissal Thrashers in arroyos was lower than those observed for shrikes in southwestern Oklahoma (Tyler 1992) and thrashers of the lower Colorado River (Finch 1982). These differences might be explained in that habitats in Oklahoma and along the Colorado River may offer greater food resources, more lush vegetation, and less severe climate than habitats in this area of the Chihuahuan Desert. Blancher and Robertson (1985) report much lower nest success rates for Western Kingbirds in southeastern Arizona than for kingbirds in uplands on our site. Western Kingbirds in this area of Arizona nested in open riparian habitats in addition to desert habitat where they overlapped breeding areas of Cassin's Kingbirds (*Tyrannus vociferans*). The increased nest density, as well as greater predation rates in the riparian habitat, may explain the differences in nest success between our study areas.

Mean clutch size for Black-throated Sparrows was significantly lower in arroyos than in uplands. Although this may be related to somewhat higher predation rates in arroyos, it suggests that arroyos lack habitat characteristics which are important for successful nesting. If uplands are

the preferred nesting habitat for Black-throated Sparrows, then inexperienced breeding adults may nest in sub-optimal arroyo habitat. This may also account for the smaller clutch sizes. All other species failed to show significant differences in clutch sizes or number of young fledged between habitats, indicating that they are equally adapted to nest in both habitats.

While over 24 species of plants were used for nesting across both habitats, they were not used equally. Little-leaf sumac, mesquite, Torrey yucca and javelina bush were used by the greatest number of bird species, even though these plants were among the lowest in density. In fact, we found no correlation between number of nests and shrub abundance. Thus, the most abundant shrub species were not used most often. Characteristics of these frequently used plant species include dense foliage, stiff branches, spinescent stems, and greater height. Each factor may offer better protection from nest predators by better concealing the nest and making access to the nest more difficult. In addition, these factors may protect nests from extreme environmental conditions (e.g., temperature) by providing more shade and by elevating nests away from the ground.

The three most abundant bird species differed in their selection of plant species for nesting. Black-throated Sparrows nested in 25 different plant species and Northern Mockingbirds nested in 13 different plant species, where as Scott's Orioles nested in only two plant species. Therefore, we classified sparrows and mockingbirds as nest-site generalists and orioles as nest-site specialists. Only mockingbirds displayed a correlation between number of nests and abundance of plant species in uplands. Thus, mockingbirds appeared to be selecting plant species for nesting that were less abundant in the habitat, whereas Black-throated Sparrows did not. Previous studies in Arizona (Tomoff 1974, Vander Wall and MacMahon 1984, Parker 1986) also found that nesting birds selected less abundant plant species as nest substrates. Because mockingbirds are considerably larger than sparrows, they may be more restricted to the larger plant species, which are rarer in the habitat. Black-throated Sparrows, however, are able to utilize the smaller, more abundant plants for nesting. Although we could not perform rank correlation analysis on Scott's Orioles because of sample size restrictions, the two plant species they selected for nesting were among the lowest in density and, thus, clearly a preferred nest substrate. Therefore, our data did not support our hypothesis that all shrub species are used equally; plant species composition, and perhaps ultimately the structural components of those plants, influences nest-site selection for some bird species.

The majority of breeding species (e.g., Western Kingbird, Black-chinned Hummingbird) appear to favor one habitat over the other for nesting, while several (e.g., Northern Mockingbirds, Crissal Thrashers)

nest in both habitats. The higher density of nests and greater number of species nesting in arroyo-riparian habitat illustrate its importance to both resident and Neotropical migrants. Chihuahuan Desert breeding birds appear to be strongly influenced by plant species composition and the presence of suitable nest sites offered by specific plants in both arroyo and upland habitat. Suitable nesting shrubs tend to be those that are spinescent, contain dense foliage, and have stiff branches. The presence of appropriate nest sites offered by little-leaf sumac, mesquite, Torrey yucca, and javelina bush is a key component of breeding bird habitat in this region of the Chihuahuan Desert. Future studies should be directed towards assessing the structural components and location of these plants relative to other shrubs and how this influences nest-site selection.

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AN EXPERIMENTAL STUDY OF PREDATION ON ARTIFICIAL NESTS IN ROADSIDES ADJACENT TO AGRICULTURAL HABITATS IN IOWA

TIMOTHY M. BERGIN,[1] LOUIS B. BEST,[1] AND KATHYRN E. FREEMARK[2]

ABSTRACT.—We quantified predation on artificial nests in Iowa roadsides and examined the relationships between nest predation and characteristics of roadsides. Transects consisting of 10 nests (five in the foreslope and five the in backslope) were set up in 136 roadsides in six watersheds in south-central Iowa. Most roadsides had herbaceous vegetation with fences (67%); fewer were wooded (18%) or had herbaceous vegetation without fences (15%). Most roads were gravel (80%), and most roadsides were adjacent to row crops (63%). Average total nest predation per transect was 23% (SE = 2), ranging from 0 to 100%. Nest predation was categorized into one of three outcomes: disappearance of eggs without disturbance to the nest bowl (39%), disappearance of eggs with disturbance to the nest bowl (17%), and broken or crushed egg shell fragments in or near the nest bowl (44%). Wooded roadsides and herbaceous roadsides with fences had significantly greater nest predation than herbaceous roadsides without fences for disappearance of eggs without disturbance to the nest bowl. Backslopes had significantly greater nest predation than foreslopes for all outcome categories except the disappearance of eggs with disturbance to the nest bowl. Wooded roadsides and herbaceous roadsides with fences along the backslope may provide cover and travel corridors for mammalian predators or elevated perches for avian predators. *Received 22 Aug. 1996, accepted 27 Feb 1997.*

Nest predation is an important cause of mortality for many bird species (Ricklefs 1969, Martin 1988), especially in grassland ecosystems where predators have responded positively to human disturbance and landscape fragmentation (Warner 1994). For example, more than half of the Dickcissel (*Spiza americana*) nests in grassland and old field habitats in Kansas (Zimmerman 1984) and half of the ground nests of a southern Maine grassland bird community suffered nest predation (Vickery et al. 1992). Grasslands have been fragmented and disturbed by agriculture over much of North America, contributing to the decline of populations of grassland birds (Askins 1994, Herkert 1994) and creating a landscape mosaic of large blocks of cropland, small patches of remnant prairie or other grassed habitats, and an interconnected network of strip-cover habitats (Warner 1994). Where agriculture has become intense, grassed habitat persists primarily as strip cover such as roadsides, grassed waterways, and fencerows.

Roadside vegetation may be of critical importance to ground-nesting birds in agricultural landscapes by providing relatively undisturbed habitat

[1] Dept. of Animal Ecology, Iowa State Univ., Ames, Iowa 50011.
[2] Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3.

for nesting (Best 1986, Camp and Best 1993, Warner 1994). Roadsides have been shown to have greater avian abundance and species richness than adjacent cropfields (Camp and Best 1993, Best et al. 1995). However, evaluations of habitat quality on the basis of abundance data alone can be misleading, because the correlation between population density and reproductive success is often poor (Van Horne 1983, Vickery et al. 1992). Strip-cover habitats, such as roadsides, can serve as corridors or travel lanes for predators, interconnecting non-linear, block-cover habitats (e.g., grasslands and woodlands), which may serve as potential sources of predators (Rodenhouse and Best 1983, Moller 1989). Roadsides also may prove to be "ecological traps," which attract high densities of nesting birds but lead to low nest success because of increased nest predation (Gates and Gysel 1978, Best 1986, Warner 1994).

Compared with other roadside studies (Snyder 1974, Warner and Joselyn 1986, Warner et al. 1987, Camp and Best 1994), our study increased the sample size, broadened the geographic scope by using six different watersheds, used artificial nests instead of natural nests for more rigorous experimental control, and compared different types of roadsides adjacent to different habitats. The objectives of our study were to quantify levels and assess patterns of nest predation in Iowa roadsides, to identify potential nest predators in Iowa roadsides, and to examine the relationships between nest predation and characteristics of roadsides and adjacent habitats.

METHODS

Study areas.—We selected six Iowa watersheds for study in 1994 which represented a range of agricultural landscapes from mostly row crops to more forage/pasture, Conservation Reserve Program (CRP) land, and woodland. The topography ranged from mainly flat to steeply rolling (Prior 1991). The Bear Creek watershed in Hamilton and Story counties and the Walnut Creek (Story) watershed in Story and Boone counties are located in the relatively flat Des Moines lobe created by the Wisconsin glacier. The Buck Creek watershed in Powesheik County, the Walnut Creek (Jasper) watershed in Jasper County, the Seven Mile Creek watershed in Cass County, and the Three Mile Creek watershed in Adair and Union counties are located in the rolling Southern Iowa Drift Plain.

Differences in weather conditions among watersheds and between experimental periods (see below) could have affected nest predation, so for each watershed, the mean daily maximum temperature and total rainfall during each experimental period were quantified by using data reported from the nearest weather station or, if equidistant, the means from the two nearest stations. Temperature and rainfall data were obtained from the Iowa Dept. of Agriculture and Land Stewardship (1994).

Nest predation.—Artificial nests were set up in linear transects in roadsides, with 16 to 28 transects per watershed depending on watershed size (N = 136 replicates). Iowa roads usually demark one-mile^2 (1.7 km^2) sections, and we took advantage of this grid system to randomly locate transects within the watersheds. Only one transect was placed within each section studied; the roadside selected was randomly choosen from among the four sides of

the section. A 200-m-long buffer was maintained on each end of the roadside to minimize the effect of intersecting roads on the transect. The transect was randomly positioned between the end buffers. Transects in adjacent sections were not located along the same 1-mile segment of road to maintain the independence of each transect. Finally, transects were positioned such that they did not cross drainages, watercourses, or roadways that might have artificially divided the transect into different segments, potentially preventing predators from responding to each transect as a unit.

Each transect was 180 m long and contained 10 artificial nests at 20-m intervals along the transect. Locations of the artificial nests within the transect were alternated between a position 2 m from the road edge (foreslope) and a position next to the adjacent habitat (backslope), which was often separated from the roadside by a fence. Nests on the same side of the roadside were separated by 40 m to reduce the likelihood that a predator would find an adjacent nest after discovering an initial nest. At each nest site, vegetation and litter were scraped from a small area of the soil surface with a garden trowel. A white plastic tag (2 × 7 cm) was secured to the ground at the center of the scrape with a 16-penny nail. This marker, concealed by the nest bowl and eggs, validated the location of a nest if the nest and its contents were removed or disturbed by predators or weather. A nest bowl was fashioned from herbaceous plant material available near the nest site, and two Japanese Quail (*Coturnix coturnix*) eggs were placed in the nest bowl. The quail eggs were obtained from a game farm in late May. Eggs were refrigerated until the day they were set out. The eggs and nest materials were handled with rubber gloves, and field technicians wore rubber boots to reduce human scent. Plastic flagging, placed across the roadside opposite each nest (at least 5 m away), was used to mark nest locations without attracting predators. Care was taken to avoid disturbing the vegetation near nest sites.

Artificial nests were set up in two consecutive two-week periods from 31 May through 28 June, the main breeding season for common farmland birds in Iowa (Best 1986). To minimize bias, half of the transects for each watershed were set up in each experimental period and distributed uniformly from the upper to lower portions of the watershed. For each transect, the artificial nests remained in place for seven days and were checked only at the end of that period, thus minimizing the effects of human disturbance. We recorded the condition of the eggs and the nest bowl. If at least one egg was broken or removed, the nest fate was assigned to predation. A few nests were disturbed by weather or mowing and were not included in the nest outcome tabulation. The number of eggs lost per nest and adjacent nest losses within a transect were documented for each nest site and transect. For each transect the proportion of nests lost to predation was calculated for the foreslope, backslope, and the total transect.

Sightings, tracks, or scat of potential predators were noted whenever observed. No special means, such as hair catchers or camera setups, were used to identify predators in our study. Even though the attribution of nest predation events to specific predators is problematical, because of overlap in the egg-handling behavior of various predator species (Rearden 1951, Einarsen 1956, Trevor et al. 1991), we categorized nest predation on the basis of the physical evidence left at the nest site. The three outcome categories were: disappearance of eggs without disturbance to the nest bowl, disappearance of eggs with disturbance to the nest bowl, and broken or crushed egg shell fragments near the nest site, whether the nest was disturbed or not.

Roadside characterization.—Our study examined several roadside characteristics and their relationships to nest predation. Specifically, we asked if nest predation in roadsides was related to roadside habitat, road type, adjacent habitat, position within the roadside, roadside width, roadside depth, and height differential between the roadside foreslope and backslope. The habitat of each roadside transect was characterized on the basis of the extent

of woody cover and the presence or absence of a fence along the backslope. Categories included: herbaceous (<5% woody cover) without a fence, herbaceous with a fence, and wooded (>5% woody cover). The road type adjacent to each transect was either gravel or paved, and the habitat adjacent to each transect backslope was designated as either row crop or non-row crop (i.e., other block-cover habitats). If both habitat types were adjacent to the transect, the predominant one was used. The width, maximum depth, and height differential of each roadside were measured at the two points 60 m internally from each end of the transect; the two values were then averaged.

Statistical analysis.—Nest predation data (i.e., the proportion of nests lost per transect) for each outcome category were adjusted using the arcsine transformation to better approximate a normal distribution and stabilize the variance (Scheffe 1959, Zar 1984). Each outcome category was examined separately in the analyses described below. Statistical significance was set at $P < 0.05$. All analyses were performed with the Statistical Analysis Software 6.09 (SAS Institute Inc. 1994).

We looked for differences in weather conditions and nest predation among watersheds and between experimental periods to determine if the data could be pooled. The two weather variables and each nest predation outcome category were examined by using two-factor analyses of variance (ANOVA) (Zar 1984). If any ANOVA (including those described below) was statistically significant for a factor, a Student-Newman-Keul's (SNK) multiple range test was used to determine which classes of the factor were significantly different (Steel and Torrie 1980).

Nest predation was evaluated relative to roadside characteristics; both categorical and continuous variables were used. The categorical variables, which included roadside habitat, road type, adjacent habitat, and position in the roadside, were analyzed by using four-factor ANOVA (Zar 1984). The within transect error term was used in the F-test for position in roadside and the among transect error term for roadside habitat, road type, and adjacent habitat. The continuous variables, which included roadside depth, width, and height differential, were analyzed by using multiple regression (Draper and Smith 1981).

RESULTS AND DISCUSSION

The mean width of roadsides was 8.2 m (SE = 0.3), the mean depth was 1.3 m (0.07), and the mean height differential between the foreslope and backslope was 0.7 m (0.06); backslopes generally were lower than foreslopes. Most roadsides had herbaceous vegetation with fences (67%); fewer were wooded (18%) or had herbaceous vegetation without fences (15%). Most roads were gravel (80%), and most roadside transects were adjacent to row crops (63%).

The average total nest predation across all roadside transects was 23% (SE = 2). The disappearance of eggs without disturbance to the nest bowl comprised 39% of the total nest predation, disappearance of eggs with disturbance to the nest bowl 17%, and predation with egg shell fragments remaining in or near the nest bowl 44%. The distribution of the proportion of nests lost to predation per transect was skewed toward the low end of the scale for each outcome category (Fig. 1). Most transects had either no nests or only one nest lost to predation. Three transects, however, had at least 80% nest loss, and one suffered complete nest loss. The average

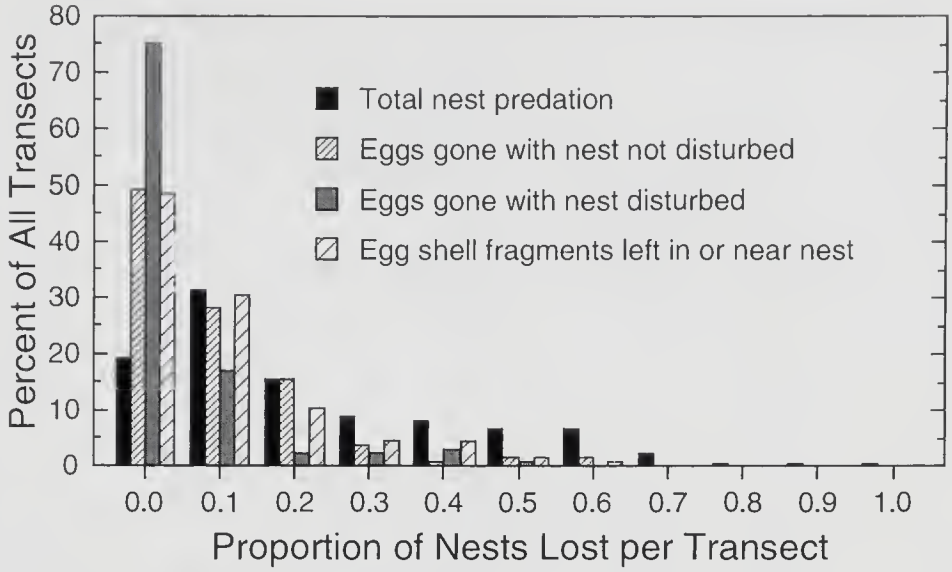

FIG. 1. The distribution of the proportion of nests lost per transect for each nest predation outcome category (N = 136).

total nest predation within watersheds ranged from a low of 14% in Walnut Creek (Story) to a high of 32% in Three Mile Creek (Table 1). The disappearance of eggs without disturbance to the nest bowl ranged from 5–15% among the six watersheds, disappearance of eggs with disturbance to the nest bowl 1–6%, and predation with egg shell fragments remaining in or near the nest bowl 4–13%.

Mean maximum daily temperature and total rainfall were not significantly different between experimental periods or among watersheds. The mean daily maximum temperature was 28°C, and the mean total rainfall was 10 cm over the entire study period. The proportion of nests lost to predation was not significantly different between experimental periods for any outcome category (Table 2). Watersheds did differ significantly in the disappearance of eggs without disturbance to the nest bowl; Bear Creek (greatest predation) and Walnut Creek (Story) (least) were significantly different from each other but not from the other four watersheds (SNK multiple range test). Given the similarity in weather conditions among watersheds and between experimental periods and the fact that only one nest predation outcome category differed among watersheds, we pooled the data in further analyses.

Most studies of nest predation in roadsides have focused on natural nests, primarily those of the Ring-necked Pheasant (*Phasianus colchicus*); nest predation in those studies ranged from 39 to 55% (Snyder 1974, Warner and Joselyn 1986, Warner et al. 1987, Camp and Best 1994). Our study had a lower average total nest predation of 23%, but showed a broad range among transects (0–100%). Our artificial nests had lower

TABLE 1

MEAN PROPORTION (STANDARD ERROR) OF NESTS LOST TO PREDATION PER TRANSECT IN FORESLOPES AND BACKSLOPES OF ROADSIDES, FOR EACH NEST PREDATION OUTCOME CATEGORY, AND FOR TOTAL NEST PREDATION

				Nest predation outcome categories[a]			
Watershed	No. of transects	Foreslope	Backslope	Eggs gone with nest not disturbed	Eggs gone with nest disturbed	Egg shell fragments	Total
Bear Creek	20	0.15 (0.04)	0.34 (0.08)	0.05 (0.02)	0.06 (0.02)	0.13 (0.04)	0.24 (0.05)
Buck Creek	28	0.08 (0.02)	0.29 (0.06)	0.10 (0.02)	0.05 (0.02)	0.04 (0.01)	0.20 (0.04)
Seven Mile Creek	28	0.21 (0.05)	0.31 (0.05)	0.09 (0.02)	0.04 (0.02)	0.13 (0.03)	0.26 (0.04)
Three Mile Creek	24	0.28 (0.06)	0.34 (0.06)	0.15 (0.03)	0.05 (0.02)	0.11 (0.02)	0.32 (0.05)
Walnut Creek (Story)	16	0.10 (0.04)	0.18 (0.07)	0.09 (0.02)	0.01 (0.01)	0.09 (0.04)	0.14 (0.04)
Walnut Creek (Jasper)	20	0.14 (0.05)	0.28 (0.07)	0.09 (0.03)	0.04 (0.02)	0.10 (0.03)	0.21 (0.06)
All watersheds	136	0.16 (0.02)	0.30 (0.03)	0.09 (0.01)	0.04 (0.01)	0.10 (0.01)	0.23 (0.02)

[a] Potential nest predators listed in order of likelihood: eggs gone with nest not disturbed—raccoon, red fox, corvids, and snakes; eggs gone with nest disturbed—raccoon, red fox, and coyote; and shell fragments remaining near nest—striped skunk, coyote, thirteen-lined ground squirrel, and mink. References for characteristics to identify predators: Sooter 1946, Rearden 1951, Einarsen 1956, and Trevor et al. 1991.

TABLE 2
RESULTS FROM ANALYSES OF VARIANCE (N = 136)

ANOVA factor	df	*F*-statistic[a]			
		Eggs gone with nest not disturbed	Eggs gone with nest disturbed	Egg shell fragments	Total
Experimental period	1	2.29	0.89	0.26	1.29
Watershed	5	2.32*	0.91	1.53	1.89
Experimental period × watershed	5	0.93	1.68	2.45*	0.69
Error	124				
Total	136				
Roadside habitat	2	3.69*	1.74	0.57	2.73
Road type	1	1.23	0.25	1.79	0.02
Adjacent habitat	1	0.92	0.49	0.91	0.15
Position in roadside	1	13.88**	0.98	8.51**	20.60**
Error (among transects)[b]	131				
Error (within transects)[c]	131				
Total	272				

[a] * = $P < 0.05$ and ** = $P < 0.01$.
[b] Error term used for roadside habitat, road type, and adjacent habitat (among transect factors).
[c] Error term used for position within roadside (within transect factor).

predation than natural nests for several possible reasons. First, our artificial nests probably had less scent than natural nests. The natural scent from incubating females was not present, and the scent from Japanese Quail females on the eggs undoubtedly had diminished in the several-week interval from laying to the setup in roadsides. This lack of scent would be most important for nocturnal mammalian predators that rely primarily on olfaction to discover nests (Whelan et al. 1994). Second, artificial nests lack the activities of adults and nestlings, such as foraging bouts and vocalizations. Avian predators such as American Crows (*Corvus brachyrhynchos*) may use adult or nestling activity as one of the cues for discovering concealed natural nests (Einarsen 1956). If true, then avian predation on artificial nests should be less than what might be expected for natural nests. In general, most predation on ground nests is mammalian rather than avian (Mankin and Warner 1992, Seitz and Zegers 1993). It is noteworthy that nest predation in our study was lower than that for two others using artificial nests in roadsides (62 and 34%; Storaas 1988, Mankin and Warner 1992). Perhaps predator densities were lower in our study, but we could not verify this.

We identified several potential nest predator species, including the raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis*

mephitis), and coyote (*Canis latrans*), from tracks left in muddy or dusty ground near transects. Canid scat also was found near some transects. Other potential nest predator species observed in the watersheds, although not necessarily near transects, included the badger (*Taxidea taxa*), thirteen-lined ground squirrel (*Citellus tridecemlineatus*), mink (*Mustela vison*), American Crow, Common Grackle (*Quisculus quiscula*), Blue Jay (*Cyanocitta cristata*), and bullsnake (*Pituophis melanoleucus sayi*).

The removal of eggs from nests with no egg shell fragments remaining near the nest bowl (55% of the total nest predation) suggests that the predators either consumed the eggs whole or carried the eggs some distance from the nest before they were consumed. Only certain nest predators are capable of these behaviors (Rearden 1951, Einarsen 1956, Best 1978, Trevor et al. 1991). Snakes are known to swallow eggs, but we have found no documentation that mammals do. Raccoons have paws capable of handling eggs and red foxes have narrow snouts that can reach into nest bowls; both are known to carry eggs away from nests. American Crows also can carry small eggs in their bills. Raccoons and red foxes are more likely to disturb the nest bowl when removing eggs than either corvids or snakes (Rearden 1951, Einarsen 1956, Trevor et al. 1991).

Broken egg shells or fragments remaining in or near the nest bowl (44% of the total nest predation) were likely attributable to either striped skunks or coyotes. Skunks cannot carry eggs and almost always leave shell fragments in or near the nest after orally extracting the contents and spitting out the shells (Rearden 1951, Einarsen 1956); coyotes break open eggs and lap up the contents (Sooter 1946). Raccoons may leave egg shell fragments but usually not at the nest site (Rearden 1951). Small mammals potentially could leave shell fragments, but studies suggest that Japanese Quail eggs are too large and(or) the shells are too thick to be readily handled by small mammals (DeGraaf and Maier 1996).

Of 307 nests lost to predation, 23% had only one egg taken, suggesting that a predator removed an egg and consumed it at another location but did not return to the nest. As noted above, several potential predators remove eggs from nests before consumption. Forty-six transects (34%) had two or more adjacent nests lost to predation, suggesting that predators such as raccoons searched for food in a directional manner by moving from one end of a transect to the other. Predation on adjacent nests was significantly more frequent in backslopes than in foreslopes (48 vs. 27% of transects with predation on that slope of the roadside; $\chi^2 = 4.54$, df = 1, $P < 0.05$).

Small-scale roadside characteristics influenced nest predation (Table 2). The disappearance of eggs without disturbance to the nest bowl was significantly greater in wooded roadsides and herbaceous roadsides with

fences than in herbaceous roadsides without fences (13 and 9 vs 3%). Backslopes had significantly greater nest predation than foreslopes for three outcome categories: the disappearance of eggs without disturbance to the nest bowl (12 vs 6%), predation with egg shell fragments remaining in or near the nest bowl (12 vs 7%), and total nest predation (30 vs 16%). Road type and adjacent habitat did not significantly affect nest predation. None of the four-factor ANOVA's showed significant interactions. The multiple regression analyses did not detect any significant relationships between nest predation and the continuous variables (roadside depth, width, and height differential).

Wooded roadsides and herbaceous roadsides with fences along the backslope may provide cover for mammalian predators and elevated perches for avian predators. Some predators such as raccoons and American Crows have affinities for wooded habitats and may be more likely to use wooded roadsides for foraging (Glueck et al. 1988, Andren 1992). The increased vertical structure and woodiness along the fences that separate the backslopes of roadsides from adjacent habitats may facilitate predator movements, which probably use the space between fences and row-crop fields as travel corridors (Rodenhouse et al. 1995). Backslopes had a greater level of adjacent-nest predation than did foreslopes, indicating either that more predators were moving along the backslopes or individual predators focused their search effort in backslopes. Foreslopes, which are more likely to be mowed (12% of foreslopes and 0% of backslopes in our study), may be avoided because predators are wary of openness and(or) human traffic on adjacent roads. Natural bird nests also are more abundant in backslopes of roadsides and the associated fencelines than in foreslopes (Camp and Best 1994), which may help explain why nest predation was more common in backslopes. If predators respond to greater nest density with increased search effort, then proportionally more nests would be located and destroyed by predators in backslopes.

The implementation of our study revealed potential limitations in its design. Although artificial nests have some advantages over natural nests in quantifying and assessing the patterns of nest predation, they also have some inherent drawbacks because artificial nests may not adequately represent natural nests (Major and Kendal 1996). One potential limitation of our study was that the inter-nest distance of 40 m may have been too short. A predator could have anticipated the next nest after discovering the initial nest(s), but we found little supporting evidence. Rarely were more than two consecutive nests disturbed. Another potential limitation was that the nest positions may have been too regularly spaced. Predators are probably better at locating nests in regular than in random patterns. Thus, our study might have been improved had we randomized the inter-

nest distances. We also placed nests in consistent positions within the roadside profile (alternating between foreslope and backslope), producing two linear groups of nests in each transect. These groups were parallel to potential travel corridors, which could have increased the likelihood of predators finding nests, especially in the backslopes. Randomizing the position of nests along the roadside cross section could have reduced this possibility. We have no direct evidence, however, that any of the above-mentioned potential limitations actually affected our results.

Our study emphasized small-scale habitat effects, but the surrounding landscape mosaic also may affect nest predation (e.g., Nour et al. 1993, Robinson et al. 1995, Yahner and Mahan 1996). Analyses at the landscape scale could provide additional insights into nest predation in Iowa roadsides.

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FACTORS AFFECTING NESTING SUCCESS IN GREATER SNOW GEESE: EFFECTS OF HABITAT AND ASSOCIATION WITH SNOWY OWLS

JEAN-PIERRE TREMBLAY,[1] GILLES GAUTHIER,[1] DENIS LEPAGE,[1] AND ANDRÉ DESROCHERS[2]

ABSTRACT.—We examined how habitat features affected nesting success of Greater Snow Geese (*Chen caerulescens atlantica*) on Bylot Island, Northwest Territories, Canada, under high (1993) vs low (1994) nesting success and colonial vs isolated nesting (1994 only). Because Snow Geese nested in association with Snowy Owls (*Nyctea scandiaca*) in 1993, we also examined the relationship between nesting success and distance from owl nests. Predation, especially by Arctic foxes (*Alopex lagopus*), was the main cause of nesting failure on Bylot Island. In 1993, goose nests near an owl nest had better success than those farther away, and they also tended to be initiated earlier. Few habitat features were related to nesting success, although nests located in pond habitat had lower success than those in wet meadows or moist tundra. In 1994, Snowy Owls were absent, and goose nesting success was much lower than in 1993 (23–42% vs 90%). Isolated nests located on hillsides had higher success than those located in lowlands. In contrast, colonial nests were more successful in lowland wet meadows, where tall willow bushes (*Salix lanata*) were present, than in either moist tundra or hillsides. In the latter habitat, nests associated with *Cassiope tetragona,* a plant that typically grows in depressions between hummocks, had higher success than those associated with other vegetation. We conclude that nesting in association with raptors, such as Snowy Owls, that maintain a predator-free area around their nest, was probably a dominant factor affecting Greater Snow Goose nesting success. In the absence of owls, isolated nests had higher success in hilly habitats than in lowlands, whereas colonial nests in tall willows were most successful. *Received 14 Aug. 1996, accepted 25 Feb. 1997.*

Predation often is the dominant factor affecting nesting success in birds and can play a major role in avian population dynamics (Wilcove 1985, Klett et al. 1988). Selection should, therefore, favor birds that use strategies or select sites that minimize the risk of predation. This is especially true in single-brooded species that do not renest after losing a clutch. In some years, nest predation by Arctic foxes (*Alopex lagopus*) causes almost complete breeding failure in tundra-nesting birds such as waders and geese (Summers and Underhill 1987, Anthony et al. 1991, Underhill et al. 1993, Ebbinge and Spaans 1995). Even though species of large body size, such as geese, may sometimes successfully defend their nest against foxes, they nonetheless suffer from predation in years of high fox

[1] Dépt. de biologie and Centre d'études nordiques, Univ. Laval, Ste-Foy, Québec G1K 7P4, Canada.
[2] Dépt. des sciences du bois et de la forêt, faculté de foresterie et de géomatique, Univ. Laval, Ste-Foy, Québec G1K 7P4, Canada.

density (Ebbinge and Spaans 1995). Several factors may affect the vulnerability of nests to predation, but one of the most important is nest concealment. Selection of habitats with increased microrelief and vegetation cover should reduce nest visibility and, thus, risk of predation in ground-nesting birds (e.g. Hill 1984, Jackson et al. 1988, Petersen 1990, Schieck and Hannon 1993).

Nesting success can vary considerably among years in arctic-nesting Greater Snow Geese (*Chen caerulescens atlantica*; Lepage et al. 1996). For instance, in 1993, many Snow Geese nested in dense colonies in association with Snowy Owls (*Nyctea scandiaca*) on Bylot Island, and their nesting success was high. In contrast, in 1994, Snowy Owls were absent and the success of geese nesting either in dense colonies or in a more isolated situation was quite low (Lepage et al. 1996). We used this opportunity to examine how habitat features affected nesting success of Greater Snow Geese under these contrasting situations: high (1993) vs low (1994) nesting success and colonial vs isolated situation (1994 only). We hypothesized that habitat features should be more related to nesting success in 1994, a year of low nesting success and of higher predator activity. A second objective was to examine the relationship between nesting success and distance from the owl nest to test the hypothesis that the high nesting success of geese in 1993 was a consequence of their association with Snowy Owls.

METHODS

Study area.—The study took place at the migratory bird sanctuary of Bylot Island, Northwest Territories, Canada. The main study area (73°08′N, 80°00′W) is a large glacial valley (hereafter called the Base-camp valley) bordered by steep hills to the north and southeast and rolling hills to the southwest. The moist upland and lowland tundra there was characterized by plants such as Arctic willow (*Salix arctica*), bell-heather (*Cassiope tetragona*), northern woodrush (*Luzula confusa*), and a sparse graminoid cover. Two wetland types associated with tundra polygons are found in the lowlands: wet meadows with a rich graminoid cover and ponds created by sunken polygons and surrounded by graminoids. In both wetland types, Fisher's dupontia (*Dupontia fisheri*), cottongrass (*Eriophorum* spp.), and water sedge (*Carex aquatilis*) were dominant plant species (Hughes et al. 1994). A secondary study area (72°53′N, 78°55′W), about 30 km south of the base-camp, was also used in 1994 (hereafter called the Camp-2 area). This area was located around a narrow valley about 0.5 km wide and surrounded by low hills with gentle slopes and extensive upland habitats. Hills were dominated by *Salix arctica* and *Cassiope tetragona*, whereas uplands were dominated by *Salix arctica* and some graminoids such as Polar grass (*Arctagrostis latifolia*). Wet meadows were found only in lowlands near the river. Graminoids were abundant in this habitat, and lanate willow (*Salix lanata*), an erect form of willow, was present.

Nesting success.—In the base-camp valley, we found nests during the laying or early incubation period by systematic searches. In the Camp-2 area, nests were found during early incubation. Nests were positioned on a map at ±25 m using a Global Positioning System receiver. A marker was located 10 m from each nest to facilitate locating nests on subsequent

visits. Nests were visited around mid-incubation, at hatch, and after hatch. Number of eggs and signs of predation (total or partial) were recorded at each visit. For nests found after the start of incubation, start of egg laying (laying date) was determined by backdating from hatching date or by estimating incubation stage based on a relationship between egg density and number of days of incubation (Lepage et al. 1996).

Nesting success refers to nests in which at least one egg hatched. We used two methods to estimate nesting success: the traditional method (number of successful nests/number of nests found) and the Mayfield method (Mayfield 1975, Johnson 1979). We present results based on the Mayfield method except in the categorical analyses which require that nests are classified as successful or failed. Results were comparable between the two methods, although the traditional method tended to over-estimate success.

Nest site characterization.—We measured habitat within 30-m of each nest. This distance was chosen because it is the average distance traveled by females from their nest during incubation recesses (Reed et al. 1995). Habitat categories differed slightly between the two study sites and years. In 1993, at the Base-camp valley, habitats were moist tundra, wet meadow, and pond habitat, all located in lowland (no nests were on hillsides). In 1994, because of small sample sizes, only two habitat types were retained in the Base-camp valley—lowland (both wet and moist) and hillside. At the Camp-2 area, habitat types were: lowland wet meadow, hillside and moist tundra. We recorded the dominant vegetation (plant species) within 30-m. In 1993, we scored within 1 m of the nest the presence of microrelief (e.g., frost heaves) or vegetation (e.g., bushes of *Salix lanata*) >15 cm in height from 0% (absent) to 100% (nest completely surrounded) to the nearest 25%. In 1994, we replaced this variable by an index of overall habitat roughness (Rodrigues 1994). Roughness was visually assessed within 30-m of each nest on a scale ranging from 1 to 3. A plot characterized by a large amount of hummocks (humps created by frost action), polygon ridges, and/or rock was rated 3; one with a few hummocks, ridges, or other relief was rated 2; flat terrain with no or little perturbations was rated 1.

Nest locations were plotted on a computer-generated map. From that, we measured the distance between each goose nest and the Snowy Owl nest that was located in the colony in 1993. In both years, nest density was estimated for each goose nest. We defined nest density as the number of nests within a 1-ha circle centered on each nest (minimum nest density according to this method was thus 1 nest ha^{-1}).

Data analysis.—We used logistic analyses to evaluate simultaneously the effect of several variables and their interactions on nesting success. These analyses treated nesting success as a binary response variable (1 = successful, 0 = failed). In 1994, an arbitrary value (0.1) was added to all cells of the contingency table to solve empty cells problem (SAS Institute Inc. 1988). We first built a general model with all variables and their interactions. Interactions were then deleted, one at a time, from higher to lower levels, until only significant interactions remained (Christensen 1990). This procedure was repeated until we reached the simplest model which still fitted the data. At each step, the reduced model was compared with the previous model with a likelihood-ratio χ^2 test (SAS Institute Inc. 1988). These analyses were performed with the CATMOD procedure of SAS.

Comparisons of Mayfield nesting success estimates were made by applying z-tests on the daily mortality probabilities as suggested by Johnson (1979). Because this procedure is a series of pairwise comparisons among different categories of a variable, the Bonferroni correction was used to adjust the significance level ($0.05/c$ where c is the number of pairwise comparisons for the study variable). α values after the Bonferroni adjustment are reported for each comparison.

We examined whether laying date and clutch size were related to distance from the Snowy Owl nest and nest density with linear regression. The effect of habitat on laying date and

clutch size was tested with an ANOVA or Kruskal-Wallis test if distribution departed from normality.

RESULTS

Causes of nest failure.—Several lines of evidence suggest that predation was the main cause of nest failure for geese on Bylot Island. First, abandoned clutches were rarely found despite frequent nest visits (only 2% of failed nests contained intact, abandoned clutches; N = 124 nests). All other nest failures occurred after all the eggs disappeared or were broken. A nest failure often occurred after partial predation, i.e. disappearance of some eggs (in 57% of nests with a visit <5 days before the failure; N = 82 nests). Second, attacks on goose nests by predators were frequently observed in all years that goose nesting activity was monitored on Bylot Island (1989–1994, except in 1993; see below). The Arctic fox was most often observed attacking goose nests. Other nest predators included the Parasitic Jaeger (*Stercorarius parasiticus*), Long-tailed Jaeger (*S. longicaudus*), Glaucous Gull (*Larus hyperboreus*), and Common Raven (*Corvus corax*).

Fox activity at the goose colonies appeared to be very different between the two years. Even though three active fox dens were found within 6 km of the goose colony in 1993, we never observed a fox in the colony during our regular nest checks. In contrast, fox activity at the goose colony was constant in 1994. We witnessed several successful attacks by foxes on goose nests at all our visits to the colony, and at least four different foxes were observed at the same time in restricted areas of the Camp-2 colony (based on variation in fur coloration).

Factors affecting nesting success in 1993.—In 1993, the only Snow Goose colony found in the Base-camp valley was located in the lowlands. Nests (N = 236) were concentrated over a 1.5-km^2 area around a Snowy Owl nest, forming a dense colony ($\bar{x}$ = 3.9 ± 0.22 [SE] nests ha^{-1}). The arithmetic center of the colony was located only 66 m from the owl nest. Overall nesting success was 89.8 ± 2.2%.

We first included all nest site variables and their interactions in the logistic analysis. However, interpretation of this general model was difficult because most of the interactions were not calculated due to missing combinations of variables. We thus preferred a reduced model (Table 1) which excluded two variables which were not significant in the general model (dominant vegetation, microrelief around the nest, and their interactions) even though it did not fit the data as well (χ^2 = 39.5, df = 25, P = 0.03). This analysis revealed that nesting success varied according to habitat type and decreased with increasing distance from the Snowy Owl nest (Table 1). However, significant interactions among variables

TABLE 1

LOGISTIC ANALYSIS OF NESTING SUCCESS IN RELATION TO HABITAT, DISTANCE FROM SNOWY OWL NEST (DISTANCE), AND NEST DENSITY AT THE SNOW GOOSE COLONY OF THE BASE-CAMP VALLEY IN 1993

Variables	df	χ^2	P
Habitat	2	6.12	0.01
Distance	1	5.02	0.03
Density	1	2.79	0.09
Habitat × distance	1	—	—[a]
Habitat × density	2	2.66	0.10
Distance × density	1	3.93	0.05
Habitat × distance × density	2	3.92	0.05

[a] Interaction not calculated due to missing categories of habitat and density. Model fit: $\chi^2 = 80.8$, df = 199, $P = 0.99$.

suggested that the effect of distance from the owl nest may vary with nest density and also among habitats.

Pairwise comparisons showed a higher nesting success (Mayfield estimate) in pond habitat (59%) than in wet meadow (93%, $P < 0.02$) and moist tundra (95%, $P < 0.02$) and a trend for lower success with increasing distance from the owl nest (95% for nests <200 m from the owl vs 87% for nests >400 m, $P > 0.05$). However, these comparisons may be affected by the interaction between habitat and distance from the owl nest because habitats were distributed unevenly within the colony, with pond habitat occurring mostly at the periphery of the colony. To control for that, comparisons among habitats were repeated using only nests located in the range of distance from the owl where the three habitats were represented. Differences among habitats were similar (Table 2), although no longer significant ($P > 0.14$), possibly because of small sample size. The effects of distance from the owl nest and density were also examined, excluding pond habitat, and both factors were again not significant (Table 2). However, pairwise comparisons are less powerful because, unlike the logistic analysis, they treat distance as a categorical variable, thus losing information.

We examined the effect of the previous variables on other components of reproduction. We found a weak but significant relationship between laying date and distance from the Snowy Owl nest as early-nesting geese tended to settle closer to the owl nest than late nesting ones (Fig. 1). Based on the number and size of young hatched in the owl nest in early July, we estimated that it was initiated around 20 May, 10 days earlier than the first goose nest (assuming a laying rate of one egg every other day and a 32-day incubation period starting on the day the first egg is

TABLE 2

MAYFIELD NESTING SUCCESS (%) OF SNOW GOOSE NESTS ACCORDING TO HABITAT, DISTANCE FROM SNOWY OWL NEST, AND DENSITY AT THE COLONY OF THE BASE-CAMP VALLEY IN 1993

Variables	N	Nesting success $\bar{x}$	SE
Habitat[a]			
Pond	15	58.8 A[b]	15.8
Wet meadow	23	88.2 A	7.8
Moist tundra	21	100.0 A	0
Distance to owl nest[c]			
0–200 m	70	95.0 A	2.8
200–400 m	73	93.6 A	3.0
400–1000 m	56	92.8 A	4.0
Nest density			
1–2 nests ha^{-1}	82	95.2 A	2.7
3–5 nests ha^{-1}	58	92.0 A	3.8
6–14 nests ha^{-1}	60	94.2 A	3.2

[a] This analysis was restricted to nests in the range of distance (445–890 m) from the owl where all three habitats were represented because of the significant interaction between habitat, nest density and distance from the owl nest (see Table 1).
[b] Means with the same letter do not differ significantly ($\alpha = 0.02$) within each variable.
[c] Nests from the pond habitat were excluded because of the significant interaction between habitat, nest density, and distance from the owl nest (see Table 1).

laid in Snowy Owls; Parmelee 1992). We also found a weak inverse relationship between laying date and nest density ($r^2 = 0.03$, $P = 0.03$, N = 236). However, this observation may not be entirely independent from distance to the Snowy Owl nest as suggested by the correlation between distance and density (Spearman $r = -0.69$, $P < 0.001$). There was no difference in laying date among habitats (ANOVA; $P = 0.86$). Clutch size was not related to distance from the Snowy Owl nest ($P = 0.44$) nor to nest density ($P = 0.52$) and did not differ among habitats (Kruskal-Wallis; $P = 0.56$).

Factors affecting nesting success in 1994.—In 1994, we found only 51 nests in the Base-camp valley. Most of these nests were isolated and scattered throughout the study area (mean density: 1.08 ± 0.04 nests ha^{-1}), and their success was very low ($\bar{x} = 23.1 \pm 6.9\%$). At the onset of incubation, a large goose colony (>2000 nests) was found 30 km south of the base-camp (Camp-2 area). A sample of nests (N = 269) was monitored at this colony. Density was high ($\bar{x} = 6.80 \pm 0.20$ nests ha^{-1}), but success also was low ($\bar{x} = 42.0 \pm 3.6\%$). No owls were found nesting in either study area in 1994. Snow melt was early in both 1993 and 1994,

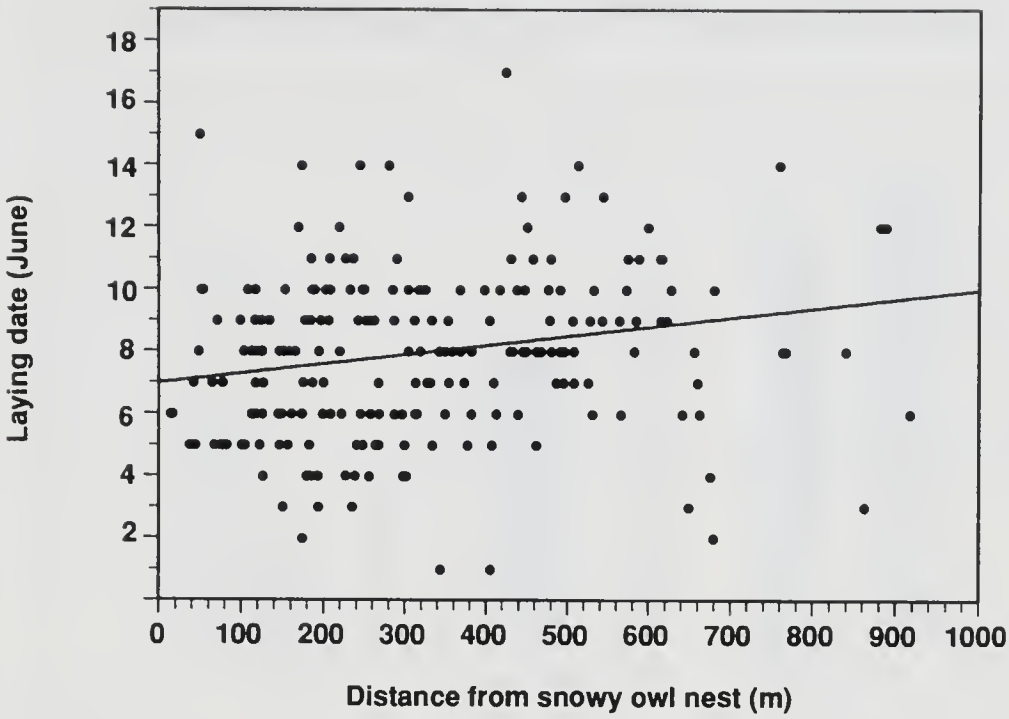

FIG. 1. Snow Goose egg laying date in relation to distance from the Snowy Owl nest at the colony of the Base-camp valley in 1993. Y = 3.0E − 3X + 156.0, r^2 = 0.04, P = 0.005 (in the regressions, X is expressed in Julian date).

and thus the effect of snow cover on nest site availability was probably minimal in both years.

Logistic analysis was not done for the Base-camp valley in 1994 because of small sample size. Pairwise comparisons of the Mayfield nesting success revealed that hillside nests had much higher success than lowland nests ($\bar{x}$ = 40.1 ± 10.3%, N = 33, vs 1.5 ± 2.2%, N = 14; $P < 0.05$). Nesting success did not vary among different categories of vegetation or habitat roughness around the nest.

At Camp-2 colony, we first built a general model with all the variables and their interactions, using the logistic analysis. A reduced model, excluding all non-significant interactions, fitted the data as well (χ^2 = 28.5, df = 57, P = 0.99) and was thus retained (Table 3). This analysis revealed that habitat roughness significantly affected nesting success, whereas the effect of habitat approached significance (P = 0.07), but vegetation and density had no effect (Table 3). However, there was a strong interaction between habitat and the dominant vegetation. Pairwise comparisons of the Mayfield nesting success showed that success was lower in medium roughness habitats than in low or high roughness, but sample size in low roughness habitats was low (N = 8; Table 4). Nesting success was higher in wet meadows than on hillsides and moist tundra, and nests located in

TABLE 3

LOGISTIC ANALYSIS OF NESTING SUCCESS IN RELATION TO HABITAT, DOMINANT VEGETATION, HABITAT ROUGHNESS, AND NEST DENSITY AT THE SNOW GOOSE COLONY OF THE CAMP-2 AREA IN 1994[a]

Variables	df	χ^2	*P*
Habitat	2	5.45	0.07
Vegetation	3	1.30	0.73
Roughness	2	6.25	0.04
Density	1	1.86	0.17
Habitat × vegetation	6	18.74	0.005

[a] Model fit: $\chi^2 = 29.1$, df = 58, $P = 0.99$.

TABLE 4

MAYFIELD NESTING SUCCESS (%) OF SNOW GOOSE NESTS ACCORDING TO HABITAT, DOMINANT VEGETATION, HABITAT ROUGHNESS, AND NEST DENSITY AT THE COLONY OF THE CAMP-2 AREA IN 1994

Variables	N	Nesting success	
		$\bar{x}$	SE
Habitat			
Hillside	71	29.8 A[a b]	6.0
Moist tundra	176	45.8 A	4.4
Wet meadow	22	85.0 B	9.8
Vegetation			
Salix arctica	96	31.8 A[c]	5.4
Cassiope tetragona	105	45.0 A	5.8
Salix lanata	10	100.0 B	0.0
Others	58	35.8 A	7.1
Roughness			
Low	8	78.2 A[b]	19.4
Medium	142	33.5 B	4.5
High	119	51.1 A	5.6
Density			
1–5 nests ha^{-1}	121	48.5 A[d]	5.5
6–20 nests ha^{-1}	146	37.3 A	4.7

[a] Means with the same letter do not differ significantly within each variable.
[b] $\alpha = 0.02$.
[c] $\alpha = 0.008$.
[d] $\alpha = 0.05$.

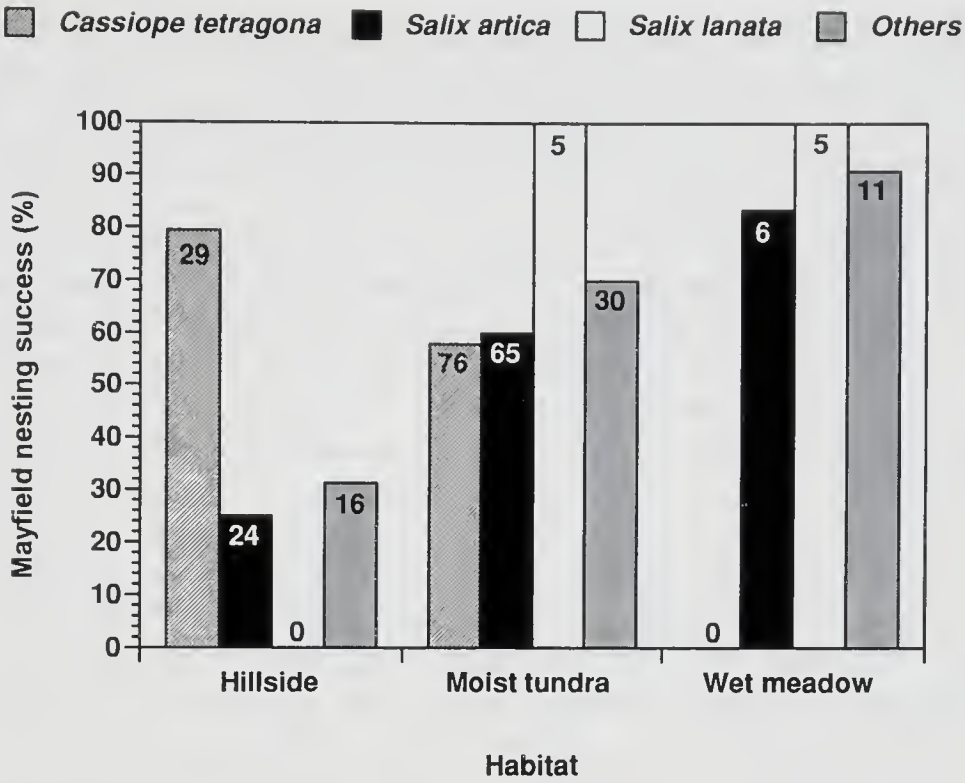

FIG. 2. Mayfield nesting success according to habitat and dominant vegetation at the Snow Goose colony of the Camp-2 area in 1994. Numbers inside the bars are sample size (a zero indicates that no nests were found in this combination of habitat and vegetation).

Salix lanata were more successful than those associated with other vegetation (Table 4). The source of the habitat × vegetation interaction appeared to be the high success of nests associated with *Cassiope tetragona* compared with those associated with other plant species in the hillside habitat but not in the moist habitat (Fig. 2).

In contrast to 1993, we found no relationship between laying date and nest density in 1994 (Camp-2 colony only) nor between clutch size and nest density (all $P > 0.1$). Laying date did not differ among habitats (Kruskal-Wallis; $P = 0.92$), although clutch size tended to be higher in wet meadow ($\bar{x} = 4.1 \pm 0.2$) than in the two other habitat types (hillside: 3.4 ± 0.1, upland: 3.6 ± 0.1; $P = 0.07$).

DISCUSSION

Association with Snowy Owl.—Lepage et al. (1996) suggested that the high nesting success of geese in 1993 compared to other years, and especially 1994, was related to their nesting association with Snowy Owls. The decrease in nesting success with increasing distance from the owl nest in 1993 further supports this hypothesis. Although this effect may be confounded by a density effect (i.e., nest density was higher near the

owl nest), the absence of nest density effect in 1994 suggests that distance from the owl was the dominant factor in 1993. It is also interesting to note that the few nests clustered around a Rough-legged Hawk (*Buteo lagopus*) nest in 1994 had a high success compared to the other nests that year (Lepage et al. 1996).

Nesting associations with Snowy Owls and Rough-legged Hawks have been reported for Snow Geese on Jenny Lind Island, Canada, and Wrangel Island, Russia, and for Brant (*Branta bernicla*) on Taimyr Peninsula, Russia (Parmelee et al. 1967, Litvin et al. 1985, Dorogoi 1990, Syroechkovskiy et al. 1991, Summers et al. 1994). This suggests that nesting in association with raptors is a strategy used by some geese to increase their nesting success. Association of geese with owls was widespread on Bylot Island in 1993 (Lepage et al. 1996). The first geese to settle at the colony also tended to be closer to the owl nest which was initiated before the geese arrived. Nesting near owl nests can be an effective anti-predator strategy for geese because owls chase off predators such as foxes, thus maintaining a predator-free area around their nests. One of us (JPT) observed an owl attacking an Arctic wolf (*Canis lupus*) 750 m from its nest and successfully chasing it. Parmelee (1992:8) reported about Snowy Owls that "Individuals will attack almost anything they consider threatening to their eggs or young, up to 1 km from their nest". This agrees well with our observations that goose nesting success remained high up to several hundred meters from the owl nest (see also Summers et al. 1994). Nesting near owls entails little cost for geese because owls rarely prey on goslings (Lepage et al. 1996).

Nesting by Snowy Owls is uncommon in our study area (Lepage et al. 1996). Nesting propensity of Snowy Owls is strongly dependent on the abundance of their main prey, lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*), which undergo large cyclic fluctuations (Larson 1960, Summers and Underhill 1987, Syroechkovskiy et al. 1991, Parmelee 1992, Underhill et al. 1993). Massive reproduction of owls (Lepage et al. 1996) as well as foxes, combined with our direct observations of numerous lemmings, suggest that 1993 was a peak in lemming abundance on Bylot Island. Low nesting success of geese in the following year may have been exacerbated by high abundance of foxes following their good breeding performance in the peak lemming year, and the low abundance of lemmings, the main prey of foxes, as suggested by Underhill et al. (1993) in Brant.

Low predation rates on bird nests in years of lemming abundance has been attributed to prey switching by foxes which then concentrate their foraging effort on lemmings rather than eggs (Larson 1960, Summers 1986, Dhondt 1987, Syroechkovskiy et al. 1991, Underhill et al. 1993).

However, our results suggest that association with owls could be another important factor involved in the high nesting success of some arctic birds in years of lemming abundance.

Habitat effects.—As anticipated, few habitat-related features were associated with goose nesting success in 1993. The high success resulting from the association with Snowy Owls probably obscured most habitat effects. The low success in pond habitat may be confounded by the owl effect, because all nests located in this habitat were at the periphery of the colony, far from the owl nest. However, it is also possible that the open structure of pond habitat increases the vulnerability of nests to predation. In this habitat, nests are located on the elevated rims of polygons which may provide easy travel corridors for foxes and reduce the area that needs to be searched.

The situation was different in 1994, as any habitat-related feature that may have reduced the risk of nest predation was probably important. In the Base-camp valley, predation pressure by foxes was intense, especially for lowland nesting geese. Isolated nests located on the hills appeared to be the most successful strategy of geese under these circumstances. The rugged terrain of hillsides may have enhanced concealment of isolated nests or, alternatively, foxes may prefer to hunt in the lowlands.

When nesting colonially at Camp-2, geese were more successful in wet meadows than on hillsides and moist tundra. This suggests that high nesting density may increase the vulnerability of nests in hillsides in contrast to isolated nests. Differences in vegetation characteristics of wet meadows between the two study areas could also have contributed to high success of nests in this habitat at Camp-2. Meadows in the Camp-2 area were restricted to a narrow band near the river where *Salix lanata* bushes were abundant. All nests located in *Salix lanata,* the only plant in our study area that grows high enough (up to 50 cm) to form bushes which can effectively conceal an incubating goose, were successful. However, abundance of this vegetation in the meadows along the river also may have enhanced concealment of nests not directly associated with this plant by limiting ability of foxes to detect nests from long distances in this habitat. This may also explain the higher clutch size of nests found in meadow habitat, as better concealment probably resulted in a lower rate of partial predation. The importance of tall willows in protecting goose nests from predation has also been reported by Jackson et al. (1988) for Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting along Hudson Bay. However, the very restricted distribution of *Salix lanata* on Bylot Island limits its availability as protective cover for nesting geese there.

Increased nest concealment in hummock depressions along slopes may also account for the higher success of nests associated with *Cassiope*

tetragona in hillside habitats. *Cassiope* typically grows in depressions between hummocks that are often >15 cm deep, especially on hillsides, and it is the only regular microrelief that conceals a goose nest on the tundra. Therefore, both micro-habitat features as well as the general landscape or habitat may affect the vulnerability of nests to predation.

In conclusion, association with Snowy Owls had an overriding effect on nesting success in Greater Snow Geese, although this conclusion is largely based on detailed observations at one owl nest. In the absence of owls, both habitat and nest dispersion influenced nesting success, but their effects were variable, possibly due to variation in predation pressure.

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NEST-SITE SELECTION AND NEST-ENTRANCE ORIENTATION IN SPRAGUE'S PIPIT

GLENN C. SUTTER[1]

ABSTRACT.—Nest-site selection and nest-entrance orientation patterns in Sprague's Pipit (*Anthus spragueii*), an endemic grassland passerine that builds a domed nest on the ground were measured at nest sites and randomly selected non-nest sites, and nest-entrance orientations were compared to random, circular distributions and dawn azimuths. Pipits showed a preference for sites in dense, grassy, and relatively tall vegetation with low forb density and little bare ground, presumably because such sites offer protection against predation and heat stress. There was no significant directionality in terms of nest-entrance orientation, implying that potential thermal benefits of an east-facing nest play a limited role during nest-site selection. *Received 11 Oct. 1996, accepted 8 Feb. 1997.*

Breeding birds show a range of behaviors that can affect their survival and reproductive success, including nest-site selection (Espie et al. 1996, Woods and Cade 1996). The choice of a suitable nest site is especially important for songbirds and other short-lived species because each chick represents a potentially large contribution to life-time reproductive output. In grassland songbirds, nest-site selection is affected by factors ranging from heat stress (George et al. 1992, With and Webb 1993) to high predation risk (Martin 1993, Camp and Best 1994, With 1994), and many species have adapted by building or selecting nest sites that are sheltered and well hidden (Ehrlich et al. 1988).

Sprague's Pipit (*Anthus spragueii*) is an endemic grassland songbird that breeds throughout much of the Great Plains of North America (Owens and Myres 1973) and in grassland areas of British Columbia (McConnell et al. 1994). Singing males are uncommon in heavily grazed areas (Dale 1983) and show a preference for native grassland over fields dominated by introduced vegetation (Cody 1974, Wilson and Belcher 1989, Sutter 1996). Like other birds of the open prairie, pipits build a domed nest at the base of a dense tussock of grass, laying 4–5 eggs per clutch and requiring 22–26 d to complete incubation and nestling periods (Maher 1973, Sadler and Maher 1974, Sutter 1996). More information is required on the nesting ecology of this species, because little is known overall (Ehrlich et al. 1988) and population levels appear to be declining by 5–10% per year over much of its range (Sauer et al. 1996).

The aim of this study was to document the nest-site selection and nest-entrance orientation patterns of pipits breeding in native mixed-grass prai-

[1] Dept. of Biology, Univ. of Regina, Regina, Saskatchewan, S4S 0A2, Canada.

rie. My objectives were to determine (1) whether pipit nests are located in relatively dense vegetation, presumably for maximum protection against predation and heat stress, and (2) whether their nest entrances are oriented towards sunrise to take advantage of the morning sun and to avoid mid-day heat. To address objective one, I compared the plant species composition and vegetation structure of pipit nest sites to that of randomly selected non-nest sites. For objective two, I tested nest-entrance orientations against a random circular distribution and compared the mean entrance direction to the dawn azimuth.

METHODS

This study was conducted from 13 May–9 August 1994 and from 9 May–8 July 1995, on approximately 256 ha of native mixed-grass prairie at the south end of the Matador Provincial Community Pasture (50°41′N 107°44′W) in Saskatchewan, Canada. The site has a flat to rolling topography and is grazed annually. Native vegetation on the site is dominated by northern and western wheat grass (*Agropyron dasystachyum* and *A. smithii,* respectively), June grass (*Koelria gracilis*), and green needle grass (*Stipa viridula*). Other common plant species include snowberry (*Symphoricarpos occidentalis*), pasture sage (*Artemisia frigida*), prairie rose (*Rosa arkansana*), sedges (*Carex* spp.), and numerous forbs (Coupland et al. 1973). Plant nomenclature follows that of Vance et al. (1984) and Looman (1982).

Pipit nests were located by dragging a weighted 30-m rope over the study site and carefully searching wherever birds flushed. Nests were also found by chance and by tracking birds wearing radio-transmitters (see Sutter et al. 1996). Once a nest was located, nest-entrance orientation was measured with a compass and corrected for magnetic declination.

Two non-nest sites were examined for each nest site, to reduce variability introduced by sampling an atypical non-nest site. Each non-nest site was located by walking a random distance away from the nest (between 1 and 100 m) in a randomly chosen cardinal direction. Non-nest sites were limited to the area within 100 m of a nest to increase the chance of non-nest sites being within the nesting territory of the bird in question (see Sutter 1996).

At both nest sites and non-nest sites, vegetation structure was measured in a 0.5 × 0.5 m quadrat that was centred over the nest (in the case of the nest site) or over a suitable tussock of grass (in the case of non-nest sites). All measurements were taken after chicks had fledged or the nest had been abandoned.

The methods I used to measure vegetation structure are described in detail elsewhere (Sutter et al. 1995). Briefly, percent cover was estimated for grasses and sedges, forbs and shrubs, bare mineral soil, and litter using the Daubenmire scale (Barbour et al. 1980). Forb density was measured by dividing the quadrat into four equal subquadrats and measuring the distance between the center point and the nearest forb in each subquadrat. These measurements were then converted to a density (D) estimate using the equation: $D = (2(d)^2)^{-1}$, where d = the mean distance in meters and 2 is a constant correction factor (Barbour et al. 1980). Vegetation density in the vertical plane was measured in each subquadrat by counting the number of plant contacts above and below 10 cm along a thin (2 mm diameter) metal rod placed randomly within each subquadrat. Litter depth and maximum plant height were estimated, respectively, by measuring the depth of loose (unattached) dead vegetation and the height of the tallest plant in each subquadrat, excluding influoresences. I also estimated the distance to the nearest potential perch, generally a shrub or rock.

In 1995, I examined plant species composition at nest sites and non-nest sites by identifying vascular plant species (sedges were identified to genus) and estimating their percent

TABLE 1

MEANS AND STANDARD ERRORS (SE) FOR HABITAT STRUCTURE VARIABLES AT SPRAGUE'S PIPIT NEST SITES AND NON-NEST SITES BASED ON 0.5 × 0.5 M QUADRATS

Variable	Nest sites	Non-nest sites	Wilcoxon results
Grass and sedge cover (%)	52.7 (3.5)	42.2 (2.2)	***
Forb and shrub cover (%)	10.5 (1.5)	13.3 (0.8)	*
Litter cover (%)	15.2 (1.2)	14.4 (1.0)	ns
Bare ground cover (%)	16.8 (3.1)	25.1 (2.2)	***
Forb density (plant contacts · m^{-2})	55.6 (15.6)	93.1 (14.3)	**
Maximum height (cm)	27.7 (0.9)	25.6 (0.6)	**
Litter depth (cm)	2.4 (0.4)	1.9 (0.1)	ns
Contacts above 10 cm	1.1 (0.1)	0.9 (0.1)	ns
Contacts below 10 cm	3.0 (0.3)	2.9 (0.3)	ns
Nearest perch (m)	20.7 (2.2)	16.8 (1.9)	ns

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$, Wilcoxon matched pairs test, N = 47.

cover in the 0.5 × 0.5 m quadrat. Unknown species were collected and compared to herbarium specimens for identification or revisited later in the growing season when they were easier to identify. Plant species richness was determined for all vascular species and separate totals were generated by life form (grasses and sedges versus forbs and shrubs) by counting the number of species in each quadrat. Plant species diversity and evenness were estimated based on the indices developed by Hill (1973).

For each structural and floristic variable, I calculated means for the pair of non-nest sites associated with each nest site, and tested for differences between nest sites and non-nest sites with a Wilcoxon matched pairs test. I used a paired, nonparametric test because non-nest sites were selected relative to nest locations and most data sets violated the assumptions required for parametric analysis. I pooled measurements from 1994 and 1995 because there was no obvious difference in grazing pressure between years.

I examined nest-entrance orientation by applying Raylcigh's test for circular uniformity (Zar 1984) and comparing the mean entrance direction to 60°, which is the mean dawn azimuth during the breeding season at the study site (Herzberg Institute of Astrophysics, National Research Council of Canada).

RESULTS

Vegetation structure was measured at 47 nest sites and 94 non-nest sites. Nest sites had significantly higher grass and sedge cover and maximum height, and significantly lower forb and shrub cover, bare ground cover and forb density (Table 1), suggesting that pipits seek out dense, grassy vegetation during nest-site selection.

Northern wheat grass (*Agropyron dasystachyum*) was the most common grass and pasture sage (*Artemisa frigida*) was the most common forb at both nest sites and non-nest sites (Table 2), and northern wheat grass often formed all or most of the nest canopy (pers. obs.). There were no significant differences between nest sites and non-nest sites in terms of

TABLE 2

MEANS AND STANDARD ERRORS (SE) FOR PLANT COMMUNITY PARAMETERS AT SPRAGUE'S PIPIT NEST SITES AND NON-NEST SITES BASED ON 0.5 × 0.5 M QUADRATS

Variable	Nest sites	Non-nest sites	Wilcoxon results
Community parameter			
Grass and sedge species richness	3.9 (0.2)	3.9 (0.1)	ns
Forb and shrub species richness	4.3 (0.4)	4.8 (0.3)	ns
Total plant species richness	8.2 (0.4)	8.7 (0.3)	ns
Plant species diversity	4.4 (0.2)	4.8 (0.2)	ns
Plant species evenness	0.77 (0.02)	0.78 (0.01)	ns
Grasses and sedges (%)			
Agropyron dasystachyum	18.8 (2.4)	13.4 (1.6)	ns
Agropyron smithii	4.5 (0.8)	4.0 (0.6)	ns
Carex spp.	6.8 (1.5)	8.9 (1.5)	ns
Koelaria gracilis	8.0 (1.6)	11.1 (1.4)	ns
Forbs and shrubs (%)			
Achillea millefolium	2.9 (1.0)	1.8 (0.4)	ns
Artemesia frigida	6.8 (1.3)	6.7 (0.9)	ns
Phlox hoodii	1.1 (0.3)	3.1 (0.8)	*

* $P < 0.05$, Wilcoxon matched pairs test, N = 21.

plant species richness, diversity or evenness (Table 2), suggesting that plant community parameters are not directly involved in nest-site selection. There were also no differences between nest sites and non-nest sites in terms of dominant plant cover, except that nest sites had slightly less cover due to moss phlox (*Phlox hoodii*). This difference is probably not biologically significant, however, since it involved only a very small amount (2%) of the vegetation cover (Table 2).

The mean (± SE) entrance-orientation of pipit nests was 82 ± 36° (N = 49, Fig. 1), which is not significantly different from the average dawn azimuth at Matador during the breeding season (95% confidence interval = 13–152°). This result should be viewed with caution, however. The distribution of the nest-entrance data was statistically uniform (Rayleigh test of circular uniformity, $P > 0.05$), indicating no strong directionality in the entrance orientation of pipit nests and little, if any, effect due to the dawn azimuth.

All of the nests examined here were also used in a larger study of pipit incubation behavior which addressed the effects of disturbance and nest-site manipulation (see Sutter 1996). As a result, I was unable to determine whether nest-site vegetation parameters and (or) nest-entrance orientation had any direct impact on nesting success.

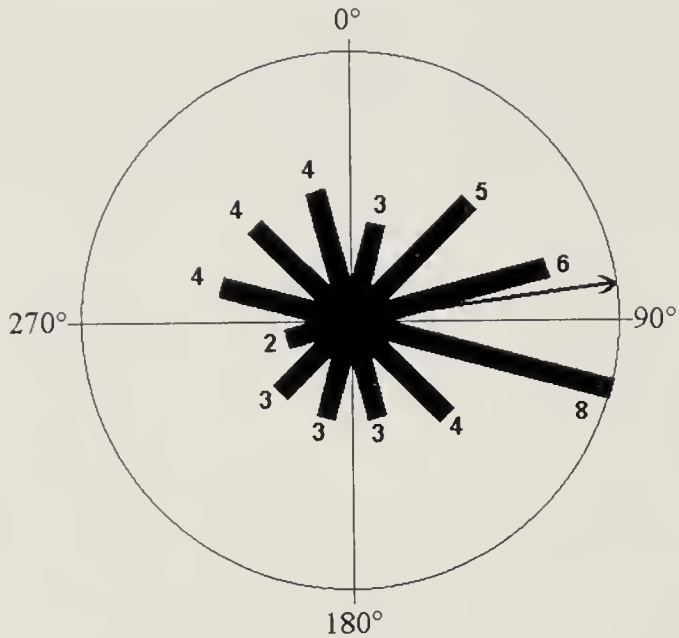

FIG. 1. Circular histogram of entrance directions for Sprague's Pipit nests. Numbers associated with each bar indicate the number of entrances that were pointing toward each direction. The overall mean direction (82°) is indicated by the arrow.

DISCUSSION

Sprague's Pipit nest sites tended to be in dense, grassy and relatively tall vegetation with relatively low forb density and low bare ground cover (Table 1). All nests were completely or partially domed, and the canopy was often comprised of northern wheat grass (*Agropyron dasystachyum*). This plant may have been an integral part of pipit nest canopies by chance, given that it was the dominant grass on the study site (Coupland et al. 1973, Sutter 1996). Alternatively, pipits may seek out this plant species because it provides abundant litter and tends to form rather loose tussocks (pers. obs.). A preference for certain plants has been shown in Tree Pipits (*Anthus trivialis*) which place their nests at the base of the grasses *Calamagrostis epigeos* and *Brachypodium silvaticum* (Loske 1987).

The thermal importance of nest cover has been recognized for some time (Wiens 1974, Walsberg 1981). Domed, well-hidden nests are used by other ground-nesting birds (Norment 1993, With and Webb 1993, Haggerty 1995) and several congeners (Verbeek 1981, Högstedt 1978, Loske 1987), presumably because ground-level microclimates can get very hot (Salzman 1982, Vispo and Bakken 1993, Sutter 1996). Nest canopies can also be beneficial at night because the vegetation limits heat loss and emits 20–30% more long-wave radiation than the night sky (Walsberg 1985).

A well-hidden nest site may also reduce (Wray and Whitmore 1979, Norment 1993), increase (With 1994), or have no effect on predation (Howlett and Stutchbury 1996), depending on the types of predators in a system and the hunting techniques they use (Martin 1993). Common songbird predators at Matador include coyotes (*Canis latrans*) and predatory birds, which hunt at least partly by sight (Maher 1974, pers. obs.), so domed nests may be an effective way for pipits to reduce the risk of predation in this area. Also, pipits may tend to avoid placing their nests in areas with high bare ground cover (Table 2) to reduce the chances of being detected by a predator as they travel to and from the nest.

Other studies have shown a connection between predation risk and the orientation of ground-level nests. Högstedt (1978) redirected the entrances of Tawny Pipit (*A. campestris*) nests from northeast-northwest to southwest and found a concomitant increase in predation. The proposed explanation was that the contents of nests facing southwest were more illuminated by sunlight and, therefore, more obvious to flying predators. Haggerty (1995) used the same argument to explain nest directionality in Bachman's Sparrows (*Aimophila aestivalis*), which nest in forest openings and tend to aim the entrance north or northeast. Significant directionality has also been reported for Water Pipits (*A. spinoletta*; Verbeek 1981) and Tree Pipits (Loske 1987).

The absence of strong nest-entrance directionality in Sprague's Pipit (Fig. 1) may be due to the fact that nests of this species are often at the end of a partially or completely covered runway which can be up to 15 cm long and sharply curved (pers. obs.). The extra shelter afforded by the runway cover may ensure that the nest contents are rarely illuminated or overheated by the mid-day sun. In contrast, nests of Tawny and Water pipits have been described as "partly covered" (Högstedt 1978) and "overhung by sod or rock" (Verbeek 1981) or even "open" (Rendell and Robertson 1994). Presumably, sunlight is able to penetrate such nests for at least part of the day, putting selective pressure on birds to optimize the orientation of the nest entrance.

In conclusion, Sprague's Pipits appear to be selective in choosing their nest site, showing a preference for more protected locations and little regard for plant species composition. I found no strong directionality in the orientation of their nest-entrance, presumably because the nest is often placed at the end of a covered runway.

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COWBIRD SELECTION OF BREEDING AREAS: THE ROLE OF HABITAT AND BIRD SPECIES ABUNDANCE

DANIEL R. EVANS[1,2] AND J. EDWARD GATES[1]

ABSTRACT.—We investigated the use by Brown-headed Cowbirds (*Molothrus ater*) of five forest edge types and the forest interior of Green Ridge State Forest in the ridge and valley physiographic province of Maryland. Habitats were sampled, and breeding birds counted at each site. Cowbirds were detected in all habitats except forest interior; occurring most frequently in forest-brush (50.0% of points), -stream (46.3%), and -powerline (33.3%) edges. Among edge types, snag BA was also significantly ($P < 0.01$) higher at forest-powerline, -brush, and -stream edges than at forest-open road and -closed road edges. These habitats had high total vegetation volume (TVV), with which bird and host species abundances were positively associated. However, high TVV was not always indicative of high snag BA. With all habitats combined, bird species abundance, total vegetation volume (TVV), and foliage height diversity (FHD) at a height of 1–2 m were significantly ($P < 0.05$) higher at points where cowbirds were detected than at those where they were not detected, however only bird species abundance remained significant ($P = 0.059$) when forest interior was removed from the analysis. We propose that cowbirds in western Maryland select breeding areas based on: (1) distinct visible edges formed by canopy openings in the forest landscape, (2) occurrence of both high snag BA and high TVV at the forest edge, and (3) presence of high bird species abundance. *Received 17 Aug. 1996, accepted 20 Mar. 1997.*

Birds nesting near habitat edges often are subjected to increased brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Brittingham and Temple 1983). Cowbirds also have been found deep within the interior of large blocks of forest, presumably searching for host nests (Chasko and Gates 1982, Verner and Ritter 1983, Gates and Giffen 1991, Hahn and Hatfield 1995). Many Nearctic-Neotropical migrants require large blocks of forest for successful reproduction and survival (Robbins 1979, Whitcomb et al. 1981, Wilcove 1988, Robbins et al. 1989). However, these forests often are fragmented (Askins 1994). We investigated the relationship between cowbird use of different forest edge types and the forest interior of a large public forest in western Maryland. First, we characterized and compared habitat types and their corresponding bird species abundances with their use by cowbirds for breeding. Secondarily, we evaluated the relationship of different habitat characteristics and corresponding bird species abundances on the selection of breeding areas by cowbirds by comparing areas where cowbirds were present with those where they were absent.

[1] Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies, Univ. of Maryland System, Frostburg, Maryland 21532.
[2] Present address: Caribbean Conservation Corporation, 4424 NW 13th St., Suite #A1, Gainesville, Florida 32609.

STUDY AREA AND METHODS

Study area and plot selection.—We conducted this study on the 15,699 ha Green Ridge State Forest (GRSF) in eastern Allegany County, Maryland, in the ridge and valley physiographic province (Stone and Matthews 1977). GRSF is the most contiguous block of state forest in western Maryland. Elevations range from approximately 152 m along the Potomac River to about 620 m on the highest ridge. The managed forest landscape forms a mosaic of different anthropogenic features, forest types, and successional stages. Permanent corridors through the forest are formed by several road and utility rights-of-way, as well as natural stream corridors.

We sampled six habitat types: forest-powerline edge (N = 18), forest-open canopy road edge (N = 28), forest-closed canopy road edge (N = 29), forest-brush edge (N = 28), forest-stream edge (N = 28), and forest interior (≥250 m from an opening, N = 29). Forest-road edges included five open canopy and six closed canopy roads. Open canopy (canopy cover at road center <10%) roads were generally dirt and gravel, and averaged 6.0 m (±0.38 SE, N = 28) wide. Closed canopy (canopy cover at road center >90%) roads were primarily dirt, and averaged 3.7 m (±0.38 SE, N = 29) wide. Brush areas at forest-brush edges were characterized by clearcuts ranging in age from 1–10 years and in size from 2.1–23.2 ha. We included forest-stream edges along six different second order streams. Streams were 5.5 m (±0.61 SE, N = 28) wide, with an overhead canopy cover of 83-99%. The powerline corridor, averaging 45.9 m (±1.4 SE, N = 18) wide, was characterized by low shrubs, herbaceous areas, wildlife food plots, and brambles near the forest edge. Management included mowing of grass areas late in the summer by the Maryland Dept. of Natural Resources and selective herbicide application to woody vegetation by the Potomac Edison Company.

We spaced sample points to maximize independence and minimize the effects of canopy openings other than those under study. Forest-powerline edge points were separated from each other by at least 200 m; all other points were separated from each other by at least 250 m. Canopy openings other than those under study had to be ≥250 m from a sample point; therefore, not every point along a particular edge was suitable. Points were often 500 m or more apart. Locations of sample points along edges began with an initial random point followed by subsequent points along the edge; points within forest interior were randomly located.

Methods.—We made counts within a 4-h period beginning at sunrise from 20 May–26 June 1995. On average, six points representing different habitat types were counted within each time period. Sample order of habitats was rotated each day to minimize temporal biases. Point counts were done at the forest edge or boundary, except for interior points, and lasted for 10 min. An additional 10 min was specifically devoted to the detection of cowbirds (20 min total). Counts began once the sample point was reached. Bird species heard or seen at a point were tallied during the count. Counts were not conducted during rain or prolonged drizzle, heavy fog, or when wind speeds exceeded 20 kph (Robbins 1981). Point count data forms were a combination of unlimited-radius and spot-mapping methods, allowing us to mark the location of birds seen or heard in relation to the sample point and forest edge.

Habitat data were collected at sample points from 12 June–20 July 1995. The understory complexity of each plot was determined using a variation of the vertical-line intercept method (MacArthur and Horn 1969). A metric measuring rod, 18 mm in diameter × 3-m long, was used to measure total vegetation volume (TVV) (Mills et al. 1991). It was placed vertically at 2-m intervals along a 20-m straight line transect. When sampling an edge, the transect was bisected by and oriented perpendicular to the edge boundary. We counted the number of decimeter sections that contained vegetation within a 1-dm radius of the rod.

Total vegetation volume was calculated using the formula: TVV = h/10p in m^3 of vegetation/m^2 units; where h = the total number of hits in all layers at all points, and p = the total number of points. An index of foliage height diversity (FHD) was calculated by treating each meter section as a vegetation layer and using the Shannon-Weiner index $H' = -\Sigma p_i \ln p_i$, where p_i = the proportion of total hits in the ith layer. Other habitat data collected at each end (0 and 20 m) of the 20 m transect and at the sample point (10 m) included tree basal area (BA, m^2/ha) divided into deciduous, conifer, and snag (angle gauge); canopy cover (%, spherical densiometer); and vegetation height (>5 m, range finder).

Within each habitat, we calculated bird species richness using the rarefaction method (Krebs 1989) and bird and host species abundance (detections/count), leaving out the cowbird. All variables were tested for normality and, except for bird species abundance, were found not to be normally distributed. A two-way independent *t*-test and an analysis of variance (ANOVA) were used to test for differences between cowbird present (i.e., detected) and cowbird absent (i.e., not detected) points and among habitats, respectively, for bird species abundance. Variables that could not be normalized were tested using a Mann-Whitney-Wilcoxon test or a Kruskal-Wallis (KW) one-way analysis of variance based on ranks. Forest interior was removed from tests used to evaluate differences in habitat characteristics among edge habitats. If a KW or ANOVA test showed a significant difference, then an appropriate multiple comparison test was used to determine which habitats were significantly different (Siegel and Castellan 1988, StatSoft, Inc. 1994). Comparisons were also made using log-linear analysis to determine the significance of interactions among variables, especially bird and host species abundance, habitat type, and edge TVV. All statistical tests were performed using STATISTICA (StatSoft, Inc. 1994).

RESULTS

We made 1980 observations of 60 bird species, including 34 known cowbird hosts. Brown-headed Cowbirds were detected in all habitat types, except forest interior. The rank order of cowbird occurrence in edge types was forest-brush (50.0% of points), -stream (46.4%), -powerline (33.3%), -open road (14.3%), and -closed road (10.3%) edges. The cowbird ranked eleventh (2.6%) in overall species abundance, and varied from eighth most abundant in forest-brush and -stream edges to fourteenth most abundant in forest-closed road and -open road edges. Based on rarefaction, bird species richness varied from 32.0 species at forest-stream edge to 39.2 species at forest-brush edge (Table 1). Host species comprised 56.7% of all species and 77.7% of all observations. Host species richness was lowest in forest-closed road edge with 17.0 species, and highest in forest-brush and -powerline edges, both with 20.3 species (Table 1). There was no significant ($P > 0.05$) difference among habitats in bird or host species richness.

The forest-powerline edge had the highest mean bird species abundance, followed by -brush, and -open road edges (Table 1). Mean bird species abundance for forest-powerline, -brush, and -open road edges were significantly ($P < 0.05$) higher than at forest-stream, -closed road, and interior (Table 1). Mean host abundance was significantly ($P < 0.05$) higher at forest-powerline and -open road edges than forest-stream, closed

TABLE 1

MEANS (±SE) OF BIRD AND HABITAT VARIABLES SAMPLED AT THE COUNTING POINT, I.E., FOREST EDGE, BY HABITAT AT GREEN RIDGE STATE FOREST, MARYLAND

	Interior (N = 29)	Closed road (N = 29)	Open road (N = 28)	Powerline (N = 18)	Stream (N = 28)	Brush (N = 28)
Bird variable						
Species richness (rarefaction)						
Bird ($E[S_{200}]$)	34.1	33.2	38.1	36.8	32.0	39.2
Host ($E[S_{180}]$)	18.0	17.0	18.7	20.3	17.5	20.3
Abundance (#/point)						
Bird	10.00 ± 0.45^{b}	10.59 ± 0.46^{b}	13.11 ± 0.56^{a}	15.28 ± 0.53^{a}	11.18 ± 0.41^{b}	13.54 ± 0.49^{a}
Host	7.66 ± 0.34^{c}	8.66 ± 0.36^{bc}	10.25 ± 0.55^{a}	11.83 ± 0.55^{a}	9.75 ± 0.45^{bc}	9.96 ± 0.44^{ab}
Habitat variable						
Vegetation height (m)	21.62 ± 0.63^{b}	22.33 ± 0.42^{b}	17.92 ± 0.86^{c}	20.71 ± 0.94^{bc}	26.57 ± 0.77^{a}	22.14 ± 0.77^{b}
Basal area (m^2/ha)						
Deciduous	33.97 ± 1.83^{a}	22.93 ± 1.37^{b}	11.79 ± 1.65^{c}	22.50 ± 2.66^{b}	24.46 ± 2.26^{b}	21.07 ± 1.37^{b}
Coniferous	5.35 ± 1.59^{a}	0.52 ± 0.35^{b}	4.64 ± 1.23^{a}	1.11 ± 0.76^{b}	3.57 ± 1.58^{a}	0^{b}
Snag	2.93 ± 0.91^{b}	0.35 ± 0.35^{c}	0.54 ± 0.40^{c}	4.17 ± 1.16^{a}	2.32 ± 1.11^{b}	3.04 ± 0.79^{b}
Foliage height diversity (H′)						
0–1 m	0.17 ± 0.02^{b}	0.20 ± 0.02^{b}	0.27 ± 0.01^{a}	0.26 ± 0.02^{a}	0.17 ± 0.02^{b}	0.23 ± 0.02^{ab}
1–2 m	0.03 ± 0.02^{c}	0.09 ± 0.03^{bc}	0.14 ± 0.03^{b}	0.09 ± 0.03^{bc}	0.11 ± 0.03^{b}	0.20 ± 0.03^{a}
2–3 m	0.07 ± 0.03^{bc}	0.09 ± 0.03^{bc}	0.10 ± 0.03^{bc}	0.02 ± 0.02^{c}	0.14 ± 0.03^{ab}	0.22 ± 0.03^{a}
Total	0.39 ± 0.05^{b}	0.47 ± 0.04^{ab}	0.60 ± 0.04^{a}	0.62 ± 0.06^{a}	0.61 ± 0.05^{a}	0.54 ± 0.04^{ab}
Total vegetation volume (m^3/m^2)	0.41 ± 0.05^{c}	0.60 ± 0.05^{bc}	0.95 ± 0.09^{a}	0.99 ± 0.10^{a}	0.79 ± 0.08^{ab}	0.96 ± 0.08^{a}

[abc] Dissimilar letters indicate statistical significance ($P < 0.05$) among habitat types.

TABLE 2

NUMBER AND PERCENTAGE (%) OF BIRDS DETECTED WITHIN ADJACENT CORRIDOR OR BRUSH OPENING (>5 M FROM THE EDGE), ALONG FOREST EDGE (±5 M FROM THE EDGE), AND WITHIN THE FOREST (>5 M FROM THE EDGE)

	Within opening		Along edge		Within forest	
Forest edge type	No.	%	No.	%	No.	%
Closed canopy road	1	0.3	280	88.9	34	10.8
Open canopy road	0	0.0	273	71.6	107	28.4
Powerline	51	18.1	156	54.7	75	27.2
Stream	0	0.0	259	80.7	62	19.3
Brush	150	38.6	147	38.1	89	23.3

road, and interior (Table 1). Mean host abundance was significantly ($P < 0.05$) higher at forest-brush edge than interior; forest-brush edge was not significantly ($P > 0.05$) different from the other edge habitats (Table 1). Forest interior had the lowest bird and host species abundances on average. When in edge habitats, birds were detected most often close to the boundary between adjacent habitats, particularly if bordered by a road or stream (Table 2).

Total vegetation volume profiles along a transect by habitat showed a similar pattern among habitats across the forest side of a transect (0–8 m), whereas TVV at the sampling point (edge or 10 m) and across the opening side of an edge (12–20 m), if present, differed among habitats (Fig. 1). Total vegetation volume was significantly ($P < 0.01$) higher in forest-powerline, -open road, and -brush edges than -closed road edge and interior (Table 1). Total vegetation volume was significantly ($P < 0.05$) higher in forest-stream edge than interior, but did not differ between any other habitat (Table 1). Mean foliage height diversity (FHD) was significantly higher at forest-powerline, -open road, and -stream edges than forest interior (Table 1). Forest-brush and -closed road edges were not significantly ($P > 0.05$) different from other habitats. Foliage height diversity by height interval was significantly ($P < 0.05$) higher at 0–1 m in each habitat, except forest-brush and -stream edges, while levels 1–2 m and 2–3 m were similar (Table 1). Foliage height diversity was similar among meter layers for both forest-brush and -stream edges (Table 1).

Although there were significant ($P < 0.05$) differences among habitats at the sampling point (10 m) for vegetation height, deciduous BA, and coniferous BA, the only obvious relationship to cowbird use, or lack thereof, was exhibited by deciduous and snag BA. Deciduous BA was significantly ($P < 0.05$) higher within forest interior than in any other

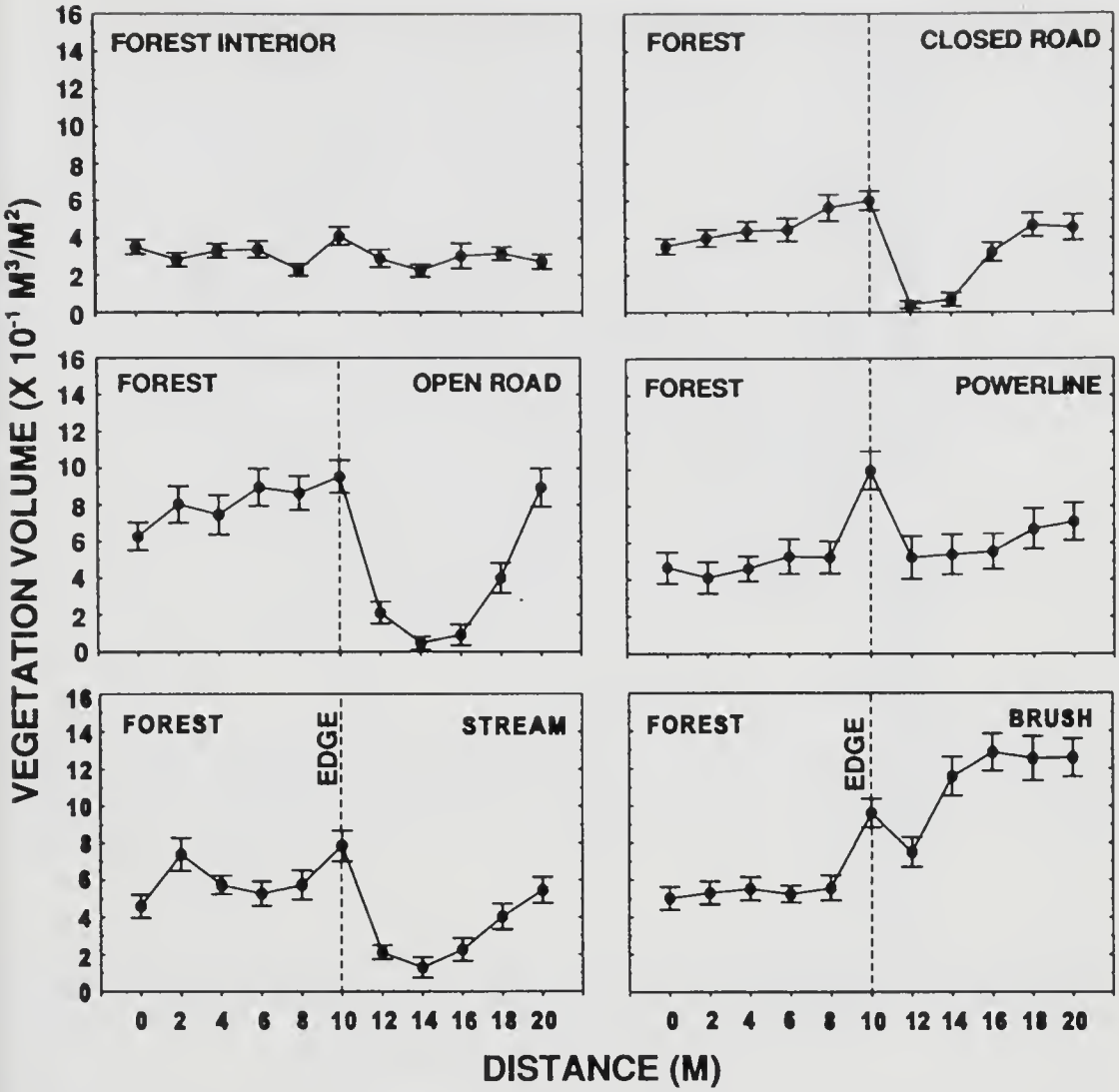

FIG. 1. Profile of mean (±SE) total vegetation volume from 0–3 m in height along a 20-m transect centered at the sampling point (10 m) within each habitat type. Except for forest interior, the transect was oriented perpendicular to the forest edge.

habitat type (Table 1). Snag BA was significantly ($P < 0.05$) higher at forest-powerline, -brush, interior, and -stream than forest-open road and -closed road (Table 1). There was generally a positive association between mean bird and host species abundance and mean TVV among habitats (Fig. 2). The response was similar for FHD. However, habitats where cowbirds were most frequently observed had both high mean snag BA and TVV (Fig. 3). Edge habitats with high mean snag BA had high mean TVV, but the reverse was not always true. Based on log-linear analysis, no relationships were detected ($P > 0.05$) among bird or host species abundance, TVV, habitat type, and cowbird occurrence. With all habitats combined, bird species abundance, TVV, and FHD at a height of 1–2 m

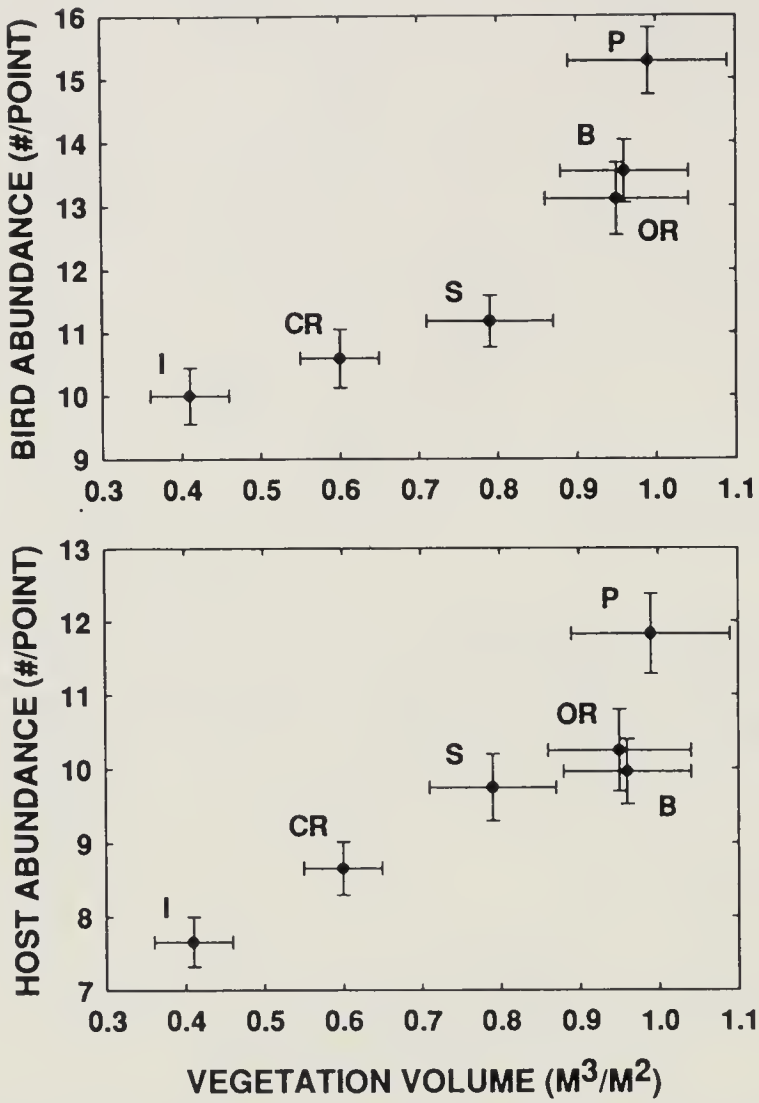

FIG. 2. The association between mean (±SE) total vegetation volume and mean (±SE) host and bird species abundances at the sampling point (10 m) within each habitat type. Habitat types are forest-brush (B), -stream (S), -powerline (P), -open road (OR), and -closed road (CR) edges and forest interior (I).

were significantly higher at cowbird present points than cowbird absent points (Table 3). However, with forest interior removed from statistical analysis and forest edge types grouped together, no significant ($P > 0.05$) difference between cowbird present and absent points occurred for host abundance, host species richness, TVV, FHD, or the abundance of any single host species. Only bird species abundance remained significantly ($P = 0.059$) higher at cowbird present points.

DISCUSSION

Because no habitat type within the anthropogenic forest landscape of western Maryland received 100% use, cowbirds in this particular region

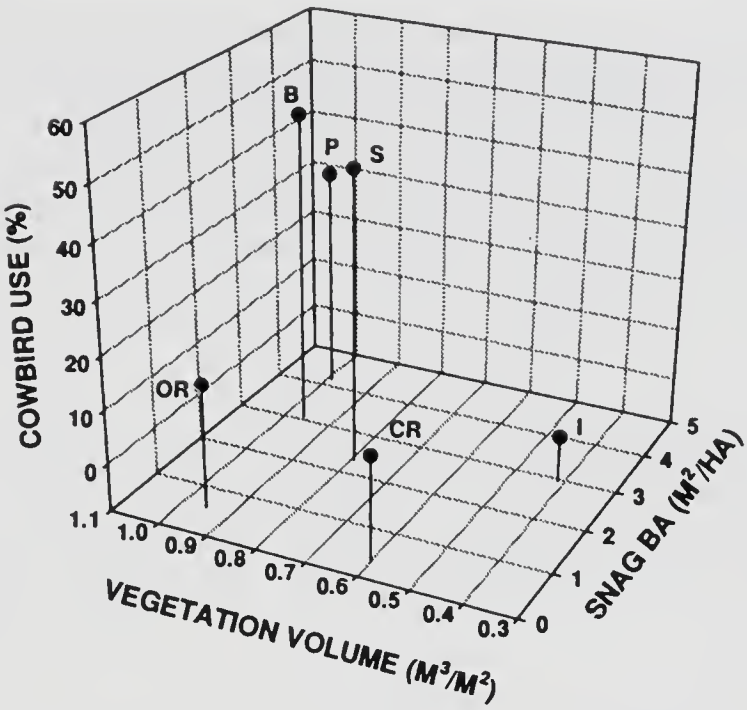

FIG. 3. The relationship between cowbird use of different habitat types and mean snag basal area and mean total vegetation volume at the sampling point (10 m). Habitat types are forest-brush (B), -stream (S), -powerline (P), -open road (OR), and -closed road (CR) edges and forest interior (I).

may be below the saturation level, selectively use only particular microhabitats, use microhabitats irregularly, or be present but undetected by an observer. However, the percentage of use of a particular habitat type should reflect its importance to cowbirds as a breeding area. Cowbirds were found near visible openings, ranging from narrow road and stream

TABLE 3

MEANS (±SE) OF VARIABLES SAMPLED AT COWBIRD PRESENT AND COWBIRD ABSENT POINTS AT GREEN RIDGE STATE FOREST, MARYLAND

Variable (units of measure)	Cowbird present	Cowbird absent	Test value
Bird species abundance[a] (detections/point)	13.23 ± 2.49 (40)	11.68 ± 3.10 (120)	2.85**†
Total vegetation volume (m^3/m^2)	0.90 ± 0.45 (40)	0.50 ± 0.43 (120)	−2.21*
Foliage height diversity for 1–2 m (H')	0.59 ± 0.25 (40)	0.51 ± 0.24 (120)	−2.05*

[a] Analyzed with an independent two-way *t*-test; all others with Mann-Whitney-Wilcoxon test. Sample sizes are in parentheses.

* $P < 0.05$; ** $P < 0.01$; † significant at $P = 0.059$ when forest interior was excluded from analysis; all others not significant.

corridors to larger clearings, and not within closed-canopy forest interior. Brittingham and Temple (1983) also reported that cowbird occurrence, and thus an increased probability of parasitism, is highest near edges and openings. Both Rothstein et al. (1980) and Verner and Ritter (1983) found higher numbers of cowbirds in open canopy plots when compared with closed canopy plots. However, this pattern may vary among landscapes and among regions (Hahn and Hatfield 1995).

An increase in bird species diversity and abundance is often related to increased vegetation layering or the amount of vegetation present in an area (MacArthur and MacArthur 1961, Swift et al. 1984, Mills et al. 1991). This relationship is especially common near permanent edges and canopy openings where there is a large difference in canopy height between habitats. At forest edges in western Maryland, TVV tended to be higher several meters into the forest than that found in forest interior, probably due to increased light penetration to all foliage layers. Furthermore, at high contrast, shrubby forest edges, nests are often concentrated near the habitat discontinuity, perhaps making these areas more productive for cowbirds searching for host nests (Gates and Gysel 1978).

Still, cowbirds did not appear to respond solely to high TVV or FHD at a forest edge in choosing a breeding habitat with high bird species abundance. Instead, it appeared that both high numbers of snags, i.e., high snag BA, and high TVV were needed for a habitat to receive high cowbird use. If one or the other factor was low, than frequency of use was also low, e.g., forest-open road edges, or nonexistent, e.g., forest interior. In other regions, snags may be an attractant to cowbirds for use as a perch while locating nests (Norman and Robertson 1975, Anderson and Storer 1976, Robbins 1979). However, in a Wisconsin deciduous forest, Brittingham and Temple (1996) found that snags near a nest did not increase its probability of being parasitized. They did find a higher percent ground cover (0–0.5 m) and number of small shrubs and saplings (0.5–1 m) at parasitized nests, which would indicate high TVV.

In western Maryland, landscape and habitat characteristics were likely the most important factors used by cowbirds in selecting breeding areas. Although the use of habitat characteristics may aid cowbirds in selecting habitat types with high host abundance, other habitat types lacking a particular characteristic but having high host abundance may receive low use. This result may be more common in regions where cowbird populations are comparatively low. Therefore, it may not always be true that cowbirds concentrate in local areas where host densities are high (Johnson and Temple 1990). Furthermore, the cowbird has a generalized reproductive strategy that is relatively insensitive to host availability, resulting in little discrimination by females among small- to medium-sized passerines

(Mayfield 1965, 1977). We propose that cowbirds are attracted to distinct visible edges formed by canopy openings in the forest landscape and, secondarily, by the occurrence of both high snag BA and TVV. These function as proximate factors directing female cowbirds to those habitats with the potential for supporting high host nest density. Once the cowbird has settled near a forest edge, the observed abundance of bird species, i.e., their activity, is likely used to further refine selection of a suitable breeding area.

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PREDICTORS OF VIGILANCE FOR AMERICAN CROWS FORAGING IN AN URBAN ENVIRONMENT

CAMILLE WARD[1,2] AND BOBBI S. LOW[1]

ABSTRACT.—We examined ways in which American Crows (*Corvus brachyrhynchos*) foraging in an urban environment balance the conflicting demands of finding food and avoiding predators. As individual vigilance (i.e., scanning) decreased, time devoted to foraging increased. Significant predictors of vigilance varied with location and included time of day, temperature, food availability, distance to nearest source of disturbance, cover distance, and size of foraging group. Group size and, secondarily, distance from cover accounted for most of the variability in vigilance. Crows were more vigilant in areas of high human disturbance than in areas of low human disturbance. *Received 21 June 1996, accepted 10 Feb. 1997.*

Vigilance (used interchangeably with scanning) and foraging are mutually exclusive behaviors—a bird cannot simultaneously scan its environment for predators while feeding. Those individuals that successfully balance the tradeoffs among various costly but beneficial behaviors will yield the greatest net benefits in terms of enhanced survivorship, reproduction, and, ultimately, increased levels of fitness (Krebs and Kacelnik 1991). Here we examined the conditions under which American Crows (*Corvus brachyrhynchos*) foraging in an urban environment are able to minimize the time spent vigilant and, thereby, maximize the time available for feeding.

Individual vigilance has most often been shown to decrease with increasing group size (Bertram 1980, Heathrote 1987, Petit and Bildstein 1987) because more eyes are thought to be available for predator detection (Pulliam 1973). Several authors have shown that vigilance is also affected by proximity to danger (Elgar 1986, Westcott and Cockburn 1988), visual obstructions in the environment (Underwood 1982, Metcalfe 1984), temperature (Beveridge and Deag 1987), food availability (Barnard 1980), time of day (Pöysä 1991), and distance to cover (Barnard 1980, Carey 1985). The objectives of this study were to determine if group size, cover distance, time of day, ambient temperature, distance to nearest disturbance, and precipitation levels were predictors of crow vigilance in urban areas with different levels of human disturbance and cover. Additionally, we examined whether vigilance varied with level of human disturbance.

[1] School of Natural Resources and Environment, Univ. of Michigan, 430 E. Univ., Ann Arbor, Michigan 48109-1115.

[2] Present address: Great Lakes Fishery Commission, 2100 Commonwealth Blvd., Ann Arbor, Michigan 48105-1563.

STUDY AREA AND METHODS

We observed crows between May 1993 and August 1993 in Ann Arbor, Michigan (42°18′N, 83°43′W), an urban college town (population 110,000) comprised of housing developments, business districts, woodlots, and open fields. In a manner established by random design (Remington and Schork 1985), data were recorded for crows foraging on green sites throughout the city. When a solitary individual or group was spotted, we waited a minimum of 5 min or until the bird(s) stopped consistent scanning in my direction before recording observations from my car, which functioned as a blind. Single crows were selected randomly from groups (Altmann 1974) without preference given to location within a group relative to other members, distance to blind or other observers, or any other correlates that could systematically bias the data. All behaviors and their duration were recorded over a 5-min. observation period. An observation period was halted if the focal bird moved out of sight, and observations less than 3 min. in length were discarded. Observation periods averaged 4.8 min. in length. Birds were watched during the breeding season, but all data pertain to adult birds. Only one bird was sampled per group, and no location was visited more than once.

Environmental variables measured included cover distance, cover type, group size, distance to nearest disturbance, level of human disturbance, time of day, level of current and previous day's precipitation, and ambient temperature. Distances to cover and nearest disturbance were initially estimated for each focal bird and, where possible, verified by pacing. Estimates were paced in 78% of the samples collected. Birds were considered part of a group if they were observed foraging together. All observations were made on small groups (one to seven individuals), with a mean distance of less than 10 m between individuals. Group members normally arrived together to feed and departed as a group. Vigilant behavior was classified as an interruption in foraging to scan the environment, and foraging behavior was classified as a peck or probe (see Remsen and Robinson 1990 for classification of feeding behaviors). Disturbance was any potential source of danger such as an observer (Elgar 1986, Glück 1987), perceived predator (Pöysä 1989), or noise. We classified level of human disturbance based partly on Mathisen (1968), taking into consideration both the extent of structural development and human activity within the vicinity of the foraging site (Table 1).

Precipitation was used as an estimate of food availability because rain induces earthworms (pers. obs.) and ground-dwelling insects to move up near the earth's surface (Villani and Wright 1988, 1990), making prey more accessible to a foraging bird. Data were collected on crows foraging on lawns or in fields for insects, a major portion of their diet during the warmer months (Good 1952). Precipitation was classified as none, light, moderate, or heavy based on duration prior to recording behavior. Light rain lasted up to one hour, moderate rain up to three hours, and heavy rain more than three hours on any given day.

Cover type was recorded as either protective or obstructive (Lazarus and Symonds 1992). Obstructive cover was opaque and minimized visibility across all planes, for example, a solid hedgerow, forest edge, or tight group of trees. Protective cover allowed maximum visibility overhead and on a horizontal plane with the foraging crow. Examples included a single tree or an open scattering of trees. Crows frequently were observed flying into protective cover. A single tree or group of trees loosely spaced should offer protection in the event of attack by a predator, but a tight cluster of trees obstructs visibility and may actually harbor a predator hidden from view (Lazarus and Symonds 1992). Observations were made on crows foraging near either protective or obstructive cover but not near both.

The independent variables group size, cover distance, time of day, ambient temperature, distance to nearest disturbance, and duration of current day's and previous day's precipitation

TABLE 1

LEVEL OF HUMAN DISTURBANCE WITHIN 0.20 TO 0.40 KM RADIUS OF A FORAGING SITE FOR AMERICAN CROWS[a]

High	Low
Built structures and roads congesting site (e.g., suburban neighborhood, downtown business district)	Built structures and roads few and scattered (e.g., agricultural setting on the edge of town)
Birds foraging in a small, isolated patch (e.g., island of grass in a parking lot)	Birds foraging in a medium/large open area (e.g., golf course, ball field)
Ratio of green space to the built environment ≤ 1:1	Ratio of green space to the built environment > 1:1
Moderate to high levels of human activity, including pedestrian traffic and human voices	Low level of human activity; one or two pedestrian sightings
Constant vehicular traffic coming from two or more sides of site	Infrequent vehicular traffic coming from no more than one side of site

[a] All five criteria in either category were given equal weight. A site had to have met three of the five criteria in either category for classification.

were measured against the dependent variable percent time vigilant for each focal bird. Because cover type and level of human disturbance did not interact to affect vigilance (two-way ANOVA, $F = 0.89$, N = 46, $P = 0.349$, square root of percent time vigilant), we examined the relationship between vigilance and the independent variables separately by level of human disturbance (N = 23 each for high and low) and cover type (N = 26 for protective, N = 20 for obstructive). Vigilance was also examined using all data pooled (N = 45, time of day not measured for one observation period) without respect to level of human disturbance or cover type. Sample sizes corresponded to the number of 5-min. observation periods recorded for analysis.

We used stepwise regression procedures (Draper and Smith 1981, Neter et al. 1990) with alpha (α) to enter and remove each variable set at 0.10 to minimize multicollinearity in the final model. Only significant variables were included in the final model. Square root transformations of the dependent variable were used to stabilize variances for regression analyses except with data from high disturbance areas, where no transformation was necessary. Regression variables were examined individually using Pearson's correlation tests (r). Except as noted, α was set at 0.05.

RESULTS

Vigilance decreased as group size, time of day, distance to disturbance, and duration of the current day's precipitation increased ($F = 14.52$, $P < 0.0005$) for crows foraging in an urban environment. The independent variables explained 59.2% of the total variability in vigilance, with group size the strongest predictor (Table 2). When the variables were examined individually, only group size was correlated with vigilance ($r = -0.60$, $P < 0.0005$, for groups containing one to seven birds). Crows that scanned less devoted more time to feeding ($r = -0.86$, $P < 0.0005$).

TABLE 2

RESULTS OF STEPWISE REGRESSION MODEL FOR OVERALL PREDICTORS OF VIGILANCE IN AN URBAN ENVIRONMENT

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Group size	−0.581 ± 0.090	36.3	<0.0005
Time of day	−0.003 ± 0.001	11.4	0.001
Distance to disturbance	−0.010 ± 0.004	6.9	0.016
Current precipitation	−0.382 ± 0.180	4.6	0.039

[a] Square root of percent time vigilant as dependent variable.
[b] Coeffecients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

In areas of high human disturbance, vigilance decreased as group size, duration of the previous day's precipitation, and current day's precipitation increased and distance from cover decreased ($F = 28.45$, $P < 0.0005$). Cover distance included both protective and obstructive cover combined, but the number of observations near protective cover was higher than the number near obstructive cover at $\alpha = 0.10$ ($\chi^2 = 3.52$, $N_1 = 16$, $N_2 = 7$, $P < 0.10$). Therefore, the positive correlation between cover distance and vigilance may actually reflect the relationship between vigilance and distance from protective cover. The independent variables explained 86.3% of the total variability in vigilance, with group size the strongest predictor (Table 3). When the variables were examined individually, only group size was correlated with vigilance ($r = -0.73$, $P = 0.001$, for groups containing one to seven birds).

Crows were also more vigilant in areas of high human disturbance than in areas of low human disturbance (ANOVA, $F = 14.78$, $P < 0.0005$, square root of percent time vigilant). Percent time vigilant averaged 21.2% in high disturbance areas and 9.5% in low disturbance areas. This

TABLE 3

RESULTS OF STEPWISE REGRESSION MODEL FOR HIGH DISTURBANCE AREAS

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Group size	−4.952 ± 0.666	54.0	<0.0005
Previous precipitation	−5.749 ± 1.148	12.6	<0.0005
Cover distance	0.228 ± 0.069	12.9	0.004
Current precipitation	−3.300 ± 1.101	6.8	0.008

[a] Percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

TABLE 4

RESULTS OF STEPWISE REGRESSION MODEL FOR LOW DISTURBANCE AREAS

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Distance to disturbance	−0.009 ± 0.003	20.3	0.014
Temperature	−0.049 ± 0.019	13.8	0.020
Group size	−0.209 ± 0.094	13.6	0.038

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

result was independent of group size, as we found no difference in mean group size between high and low disturbance areas (ANOVA, $F = 1.20$, $P = 0.27$). Group size averaged 2.6 birds in high disturbance areas and 3.1 birds in low disturbance areas.

In areas of low human disturbance, vigilance decreased as distance to disturbance, temperature, and group size increased ($F = 4.52$, $P = 0.006$). The independent variables explained 47.7% of the total variability in vigilance with distance to disturbance the strongest predictor (Table 4). Individually, none of the variables was correlated with vigilance.

When protective and obstructive cover types were combined and the overall effects analyzed, we found no correlation between cover distance and vigilance ($r = -0.03$, $P = 0.81$). When broken down, cover distance was correlated with vigilance both near protective and obstructive cover. Near obstructive cover, vigilance decreased as group size and distance to nearest disturbance increased ($F = 11.62$, $P = 0.001$). The independent variables explained 57.8% of the total variability in vigilance, with group size the strongest predictor (Table 5). Individually, only group size was correlated with vigilance ($r = -0.68$, $P = 0.001$, for groups containing one to five birds). Because of the multicollinearity between group size and cover distance ($r = 0.69$), cover distance was not incorporated in the

TABLE 5

RESULTS OF STEPWISE REGRESSION MODEL FOR AREAS NEAR OBSTRUCTIVE COVER

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Group size	−0.648 ± 0.177	46.5	0.002
Distance to disturbance	−0.011 ± 0.005	11.3	0.048

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

TABLE 6

RESULTS OF STEPWISE REGRESSION MODEL FOR AREAS NEAR PROTECTIVE COVER

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Cover distance	0.048 ± 0.009	37.9	<0.0005
Group size	−0.395 ± 0.080	28.5	<0.0005
Temperature	0.073 ± 0.027	8.2	0.014

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

multiple regression model. Examined individually, cover distance explained 20.7% of the variability in vigilance ($F = 4.70$, $P = 0.044$).

Near protective cover, vigilance decreased as cover distance and temperature decreased and group size increased ($F = 21.53$, $P < 0.0005$). The independent variables explained 74.6% of the total variability in vigilance with cover distance the strongest predictor (Table 6). Individually, only cover distance ($r = 0.61$, $P = 0.008$) and group size ($r = -0.58$, $P = 0.015$, for groups containing one to seven birds), were correlated with vigilance.

DISCUSSION

Group size, beyond all other variables measured, was the most effective predictor of vigilant behavior in foraging crows. Its prime importance in high disturbance areas may reflect an individual's assessment of its own vulnerability. Visual obstructions and increased structural complexity, characteristics of high disturbance areas, reduce the distance from which birds can visually detect predators. Escape from a predator may be less likely if a predator is able to initiate an attack closer to its prey (Metcalfe 1984). Group formation among crows foraging in high disturbance areas probably works as a form of vigilance sharing among group members. Such sharing may be especially important in high disturbance areas, where increased rates of vigilance leave less time available for feeding.

Group formation in low disturbance areas was less important than group formation in high disturbance areas as a predictor of individual vigilance. Because structural complexity and human activity is minimized in low disturbance areas, predation pressure may not be as effective a predictor of group size and vigilance; although even in areas of low human disturbance, the threat of predation is never completely removed. The similarity in group sizes between high and low disturbance areas, suggests that crows probably group together for reasons other than strictly predator detection. Kin selection, reproduction, social learning, and pos-

sibly enhancement of food acquisition all may be associated with group formation in American Crows (Kilham 1989).

Group size was a more effective predictor of vigilance near obstructive cover than near protective cover. Because good or abundant urban foraging sites may, in fact, be located near obstructive cover, group foraging might be one strategy crows employ to increase the number of foraging sites available to them without a significant increase in risk of predation. Also, because crows frequently forage within and defend a nesting territory (Kilham 1989), group formation may be one way to overcome the potential negative consequences of a territory surrounded primarily by obstructive cover. The negative correlation between cover distance and vigilance, although marginally significant, suggests that group foraging can never completely eliminate the risk of attack initiated from behind obstructive cover.

Cover distance was a more effective predictor of vigilance than group size near protective cover. Protective cover, which is minimally obstructive and less likely to harbor an undetected predator than obstructive cover, may offer a safe retreat to a crow fleeing danger. Therefore, group foraging may not be as important near protective cover as it would be near obstructive cover, especially if the birds perceive less danger or risk of attack near protective cover. My results agree with the findings of Lazarus and Symonds (1992) who found similar relationships between vigilance and distance from protective and obstructive cover types for both House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*).

Predator activity and frequency are normally greatest early in the morning (Pöysä 1989, 1991) and at night (Kilham 1989), which may account for the increased vigilance early in the day with pooled data. The indirect correlation between precipitation and vigilance indicate that crows may spend less time being vigilant when food is readily available in areas of high human disturbance. Barnard (1980) found similar results with House Sparrows which decreased scanning as seed density increased.

Distance to nearest disturbance may have been the strongest predictor of vigilance in areas of low human disturbance, because in areas with little noise, human traffic, and high visibility, crows may have been especially sensitive to an occasional noise or disturbance when it did occur. Such findings support those of Westcott and Cockburn (1988) who found that both Red-rumped Parrots (*Psephotus haematonotus*) and Galahs (*Cacatua roseicapilla*) increased scanning rates near noise, and Elgar (1986) found that House Sparrows increased scanning as proximity to human observers decreased. In high disturbance areas, with persistent noise and activity, sensitivity to individual disturbances would be difficult.

Temperature was a conflicting predictor of vigilance in areas of low human disturbance and near protective cover. Beveridge and Deag (1987) found that House Sparrows and Starlings scan more at warmer temperatures because the birds are looking for potential mates or rivals associated with reproduction; and Chaffinches (*Fringilla coelebs*) scan more at lower temperatures because the birds are watching for conspecifics who may have located a more profitable food source. The current literature on temperature and vigilance is often contradictory and does not take into account the effects of locational differences. For crows, the importance of temperature is apparent only in the context of the surrounding environment.

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BEHAVIOR OF PUERTO RICAN PARROTS DURING FAILED NESTING ATTEMPTS

KAREN A. WILSON,[1] MARCIA H. WILSON,[2] AND REBECCA FIELD[3]

ABSTRACT.—We compared patterns of nesting behavior of four pairs of Puerto Rican Parrots (*Amazona vittata*) that experienced failed nesting attempts to behavior of four pairs of parrots that experienced no substantial nest problems and successfully fledged young without management intervention. Only changes in female parrots' behavior were clearly associated with nest failure. During incubation, decreases in nest attendance, increases in duration of recesses, and increases in frequency of nest entries by female parrots were associated with imminent abandonment of nests. During early chick rearing, similar behavior was associated with the loss of broods. Low nest attendance and long recesses by female parrots during incubation were also associated with successful hatching of eggs followed by death of young several days later. The behavior patterns and changes in Puerto Rican Parrot nesting behavior described in this paper may alert biologists to nest problems that might be mitigated by management intervention. *Received 7 May 1996, accepted 12 Feb. 1997.*

The Puerto Rican Parrot (*Amazona vittata*) is critically endangered, with a minimum of 38 individuals remaining in the wild (1996 pre-breeding survey, F. Nunez-Garcia, pers. comm.). Because of such small population size, monitoring and management of the wild flock are important components of the Puerto Rican Parrot Recovery Program and are vital to the parrot's continued recovery. To maximize fledging rates in the wild, for example, biologists routinely monitor and manipulate contents of active nests when eggs or young are believed to be in jeopardy. However, Puerto Rican Parrot nests in the wild are difficult to observe because they are located in deep tree cavities and because nesting adults are sensitive to disturbance. Therefore, biologists must often rely on behavioral cues from nesting adults to determine if intervention is needed. Currently, however, few specific guidelines for identifying indicators of potential nest problems are available. Parrot managers, biologists, and nest observers (particularly new or seasonal personnel) need additional guidelines in order to maximize the effectiveness of nest monitoring and management.

The purpose of this study was to provide a detailed description of adult Puerto Rican Parrot nest attentiveness during failed nesting attempts

[1] Puerto Rico Research Group, Patuxent Wildlife Research Center, Laurel, Maryland 20708-4015 (closed 1995) (Present address: 1456 Garner Avenue, Schenectady, New York 12309).
[2] Puerto Rico Research Group, Patuxent Wildlife Research Center, Laurel, Maryland 20708-4015 (closed 1995) (Present address: Patuxent Wildlife Research Center, U.S. Geological Survey, 11410 American Holly Drive, Laurel, Maryland 20708-4015).
[3] Massachusetts Cooperative Fish and Wildlife Research Unit, Biological Resources Division, U.S. Geological Survey, Univ. of Massachusetts, Amherst, Massachusetts 01003-4220.

(those that were abandoned by the adults and those that resulted in the loss of the brood) in comparison to nest attentiveness by parrots that successfully fledged young and to identify behaviors associated with threats to reproductive success. Behavior of adult Puerto Rican Parrots during successful nesting attempts (those that involved no manipulation of eggs and fledged at least one chick without the assistance of management intervention) was described in an earlier publication (Wilson et al. 1995).

STUDY AREA AND METHODS

During the study period (1987–1990), Puerto Rican Parrots nested in four distinct valleys within the Caribbean National Forest, Puerto Rico (18°19′N, 65°45′W). All four valleys are in the Colorado Forest vegetation association described by Wadsworth (1951). Snyder et al. (1987) reported that three of the four nesting areas included in our study are 510–625 m above sea level; during 1974–1978, these areas received mean annual rainfall of 342–399 cm and had an approximate temperature range of 16–29°C. Although no data describing the fourth valley in our study area were collected, we believe it possessed characteristics similar to those described above.

We (KAW and MHW) collected data and supervised data collection by staff and volunteers in the Puerto Rican Parrot nest guard program (Lindsey 1992). Nests were monitored from dawn to dark from observation blinds during 80–94% of all days on which a nest contained eggs or chicks (Lindsey 1992). In 1989 and 1990, we also monitored vocalizations and movements within nest cavities by using a remote listening device attached to a microphone placed in each nest. More detailed methods are described in Wilson et al. (1995).

We calculated values for five behavioral components: nest attendance (for males and females), frequency of nest entries (for males and females), mean attentive period (for males and females), mean recess (females only), and longest recess (females only) for each day of the parrots' nesting cycle. Although these five behavioral components were partially interrelated, we described each component to provide a more complete description of each parrot's behavior. We divided the nesting cycle into four stages: egg laying (day −2 through 6), incubation (day 7 through 26), early chick rearing (day 27 through 47), and late chick rearing (day 48 through fledging). We then compared data from failed nesting attempts to data from successful nesting attempts described by Wilson et al. (1995).

We did not apply statistical tests to these data for two reasons. First, nesting attempts by the same pair were not truly independent. For purposes of descriptive analysis, however, we treated each nesting attempt as a separate event, because each new clutch offered the pair an opportunity to succeed or to fail in raising their young. Second, small sample size (8 successful and 5 failed nesting attempts) can lead to high probability of Type II error (Siegel 1956). Instead, we defined the behavior of pairs that experienced failed nesting attempts as different from the behavior of pairs that successfully fledged young if (1) the duration or frequency of the behavior was at least 20% greater than the upper limit or at least 20% less than the lower limit of the range of values of the behavior by parrots that successfully fledged young or (2) the pattern or trend in values was different than the pattern or trend in values by parrots that successfully fledged young.

RESULTS

Four pairs (E1, E3, S1, S2) observed during this study failed to fledge young during a total of five nesting attempts (the S1 pair experienced two

TABLE 1

BRIEF SUMMARY OF EVENTS DURING FAILED NESTING ATTEMPTS BY PUERTO RICAN PARROTS, 1987–1990

Nest problem	Nesting attempt	Day	Event
Abandonment during incubation	E1	17	Pearly-eyed Thrasher entered nest. One egg damaged.
		25	Nest abandoned. Undamaged egg (pipping) removed to the Luquillo Aviary. Attempts to foster young into nest were unsuccessful.
Abandonment during incubation	E3	18	Puerto Rican boa approached nest. Eggs (all fertile) moved to the Luquillo Aviary and replaced with artificial eggs.
		26	Nest abandoned. Attempts to foster young into nest were unsuccessful.
Loss of brood	$S1_a$	18	Intense vocal and physical interaction between breeding pair and conspecific intruders.
		45	Nest inspection. Two dead chicks partially consumed by insect larvae, one pipped egg with dead embryo. Attempts to foster young into nest were unsuccessful.
Loss of brood	$S1_b$	41	Nest inspection. One dead chick, one live chick.
		66	Nest inspection. One dead chick. No attempts to foster young into nest.
Loss of brood (Loss of female)	S2	32	Nest inspection. One dead chick, two eggs with dead embryos. Surrogate chicks successfully fostered into nest.
		71	Red-tailed Hawk lunged toward male.
		76	Female does not return to nest area. Presumed dead. Chicks removed from nest.

failed nesting attempts, $S1_a$ and $S1_b$, Table 1). Two pairs abandoned their nests during late incubation (E1 and E3). During three nesting attempts ($S1_a$, $S1_b$, and S2), two additional pairs lost their broods shortly after their chicks hatched.

We observed only minor differences during the egg-laying stage in the behavior of pairs that experienced failed nesting attempts compared to the behavior of pairs that successfully fledged young. During all stages of the nesting cycle, we observed only minor differences in the lengths of mean attentive periods of both males and females that experienced failed nesting attempts compared to lengths of mean attentive periods of those that successfully fledged young. We observed notable differences

in the remaining behavioral components during some, but not all, other nesting stages as described below.

Female nest attendance.—During incubation, females exhibited differences in nest attendance during three of five failed nesting attempts observed ($S1_a$, E3, E1) compared to nest attendance by females that successfully fledged young (Fig. 1A, B, C). During the $S1_a$ nesting attempt, the female tended to spend less time in her nest ($\bar{x}$ = 90.2% ± 0.8% SE) throughout incubation than did females that successfully fledged young (range of daily mean: $\bar{x}$ = 93.2% ± 2.2% SE to 97.4% ± 0.2% SE) (Fig. 1A). This female ($S1_a$) and the E3 female suddenly decreased their attendance during mid-incubation (days 13 and 18, respectively) (Fig. 1A, B). These decreases were associated with intense territorial defense against conspecific intruders ($S1_a$) and disturbance from a Puerto Rican boa (*Epicrates inornatus*) (E3) and resulting human activity. The $S1_a$ female returned to her previous pattern of nest attendance on day 14 (Fig. 1A). Although the E3 female generally became more attentive following the boa's visit, she exhibited a second drop in attendance just prior to abandoning her nest on day 26 (Fig. 1B). During the third nesting attempt, the E1 female exhibited a pattern of erratically decreasing nest attendance in association with numerous incidents of disturbance by predators (i.e., Pearly-eyed Thrashers, [*Margarops fuscatus*]) and resulting human activities before finally abandoning her nest (Fig. 1C).

During early chick rearing, females exhibited changes in patterns of nest attendance during two of three nesting attempts observed during this stage ($S1_a$ and S2, Fig. 1A, D). During the $S1_a$ nesting attempt, the female's pattern of attendance was comparable to that of females that successfully fledged young until day 44, when her attendance suddenly decreased (Fig. 1A). We confirmed the deaths of her young the following day. During the S2 nesting attempt, the female's attentiveness unexpectedly decreased two days before we confirmed death of her young (Fig. 1D). Following successful fostering of surrogate Hispaniolan Parrot (*Amazona ventralis*) young into the S2 nest, however, the female resumed a pattern of attendance comparable to that of successful females (Fig. 1D).

During late chick rearing, the $S1_b$ female maintained relatively high nest attendance ($\bar{x}$ = 73.6% ± 2.2% SE) compared to nest attendance of females that successfully fledged young (range of daily $\bar{x}$ = 23.4% ± 4.9% SE to 55.9% ± 8.3% SE) (Fig. 1E). The S2 female maintained nest attendance comparable to that of females that successfully fledged young until her disappearance on day 76.

Frequency of female nest entries.—During early chick rearing, the $S1_a$ female entered her nest more frequently than did females that fledged

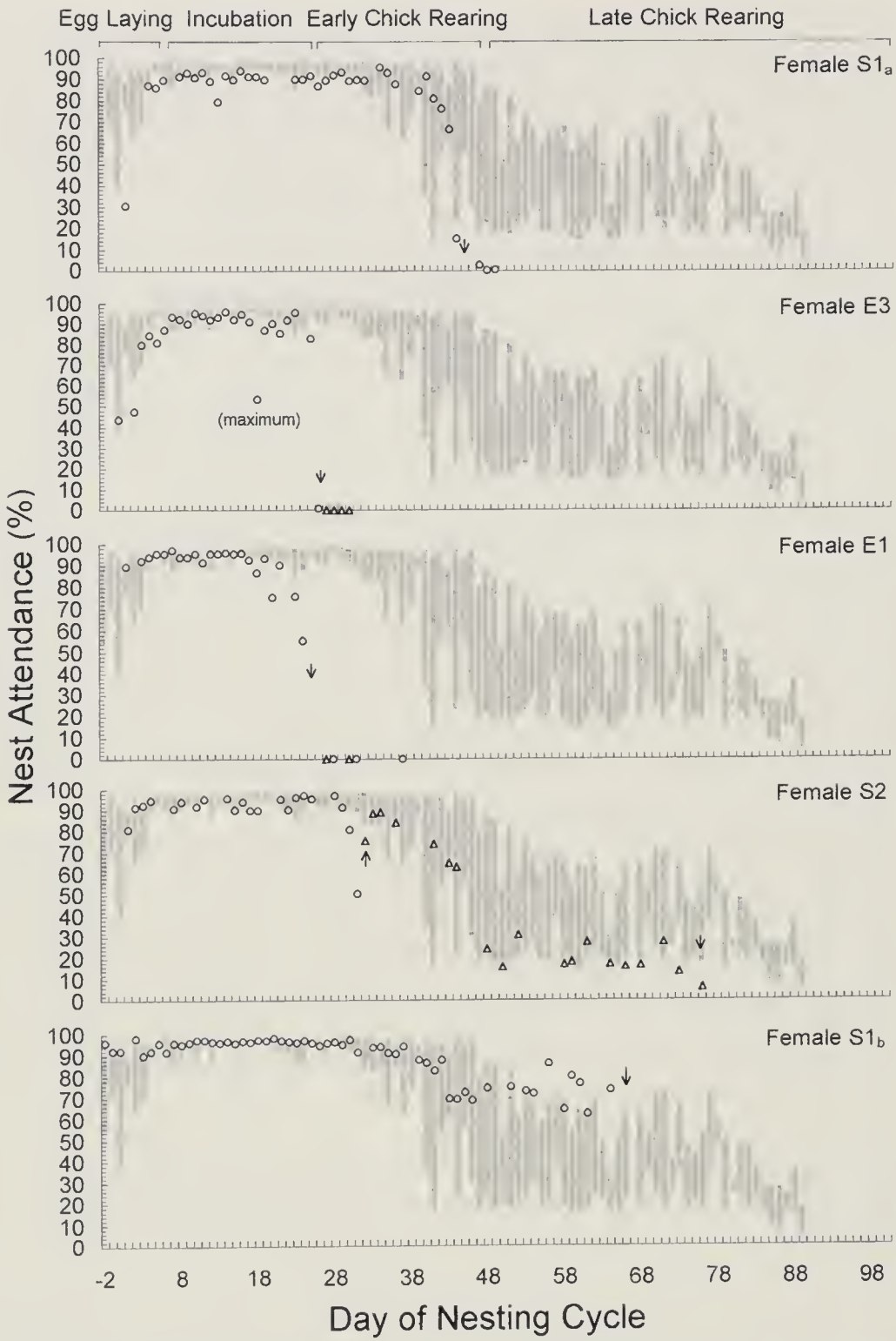

FIG. 1. Nest attendance (percentage of a 15-h period spent in nest cavity) by female Puerto Rican Parrots during failed nesting attempts (circles) shown with range (bars) of nest attendance by female parrots that fledged young, 1987–1990. Arrows indicate day that nest was abandoned or nest failure was discovered. Triangles represent behavior of parrots with surrogate young.

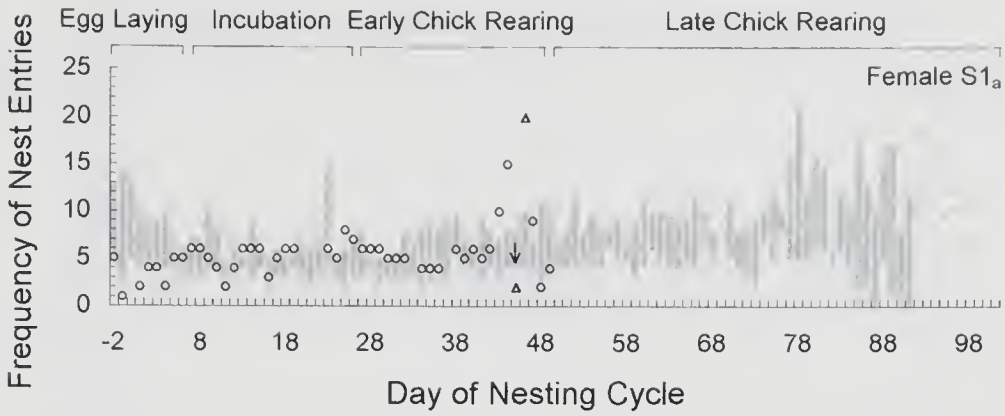

FIG. 2. Frequency of nest entries (number of visits per day) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

young (Fig. 2). The frequency of nest entries increased on day 43 and exceeded the expected range of frequency of nest entries on day 44, one day before we confirmed nest failure (Fig. 2). Her frequency of nest entries became erratic during attempts to foster surrogate young into the nest. All other females entered their nests at a rate comparable to that by females that successfully fledged young.

Female mean recess.—During incubation, females exhibited differences in mean recesses during four nesting attempts ($S1_a$, E3, E1, and S2; Fig. 3A, B, C, D, respectively) compared to mean recesses by females that successfully fledged young. During the $S1_a$ nesting attempt, the female frequently took long mean recesses ($\bar{x}$ = 17.6 min ± 1.9 min SE) throughout incubation compared to mean recesses of females that successfully fledged young (range of daily $\bar{x}$ = 5.8 min ± 0.7 min SE to 12.8 min ± 5.3 min SE). This female and one other female, E3, unexpectedly increased the length of their mean recesses during mid-incubation (days 11–13 and 18, respectively, Fig. 3A, B). The two females that abandoned their nesting attempts (E3 and E1) began to take longer mean recesses one to two days prior to abandonment (Fig. 3B, C). One female (S2) suddenly increased the average time she spent off her nest one day before we confirmed the loss of her young (Fig. 3D). Following successful fostering of surrogate young, however, this female's mean recesses were comparable to those of females that fledged young (Fig. 3D).

Longest female recess.—During incubation, females exhibited differences in longest recesses during three nesting attempts ($S1_a$, E3, and E1) compared to longest recesses by females that fledged young (Fig. 4A, B, C). During two nesting attempts ($S1_a$ and E3), females suddenly increased their longest recesses during mid-incubation (days 13 and 18 respectively, Fig. 4A, B). During nesting attempt E1, the female's pattern of longest recesses became erratic during the latter half of the incubation period (Fig.

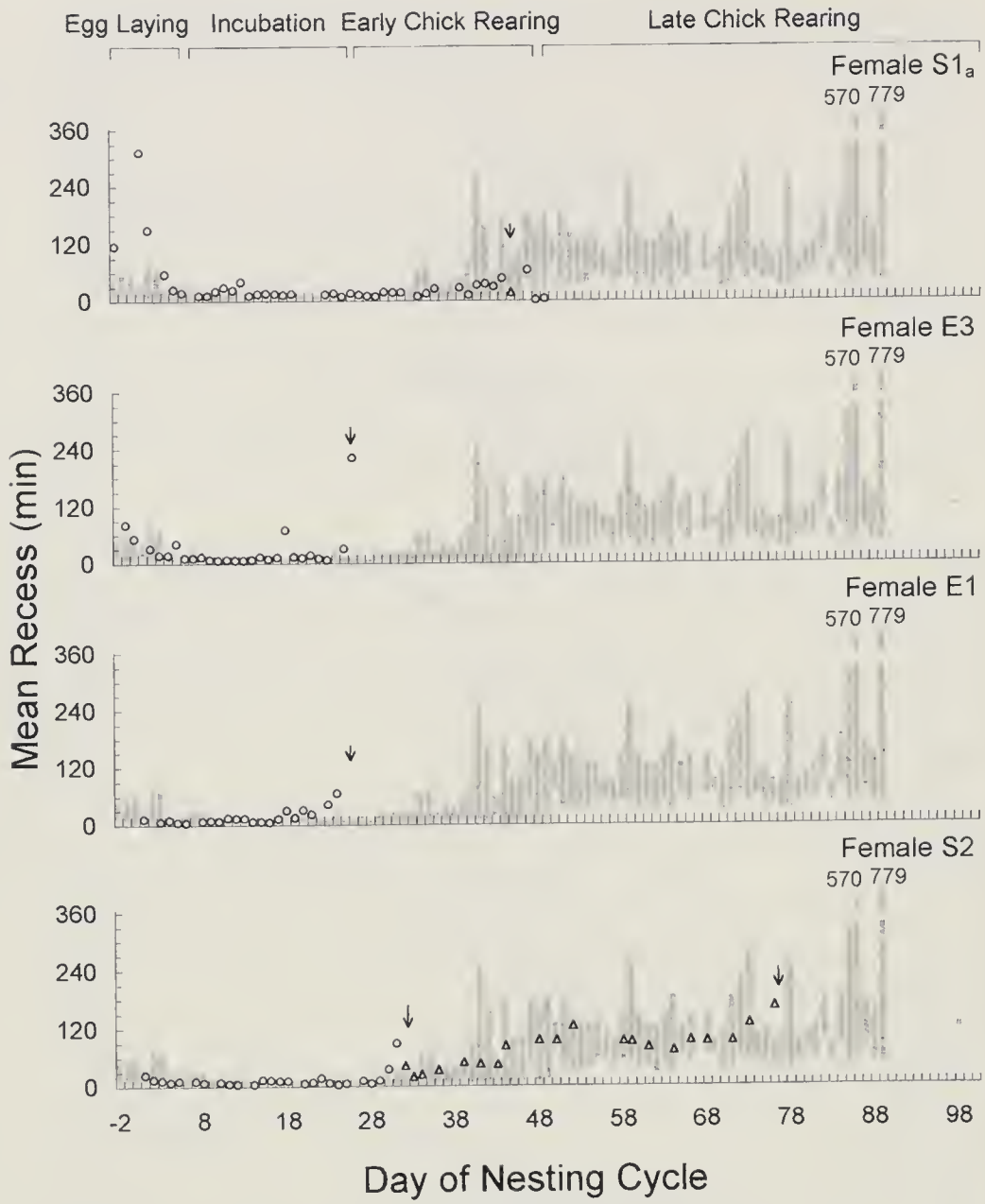

FIG. 3. Mean recesses (average period out of nest) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

4C). Both the E3 and E1 females tended to spend more time away from their nests during their longest recesses one to two days prior to abandoning their nests (Fig. 4B, C).

During early chick rearing, females unexpectedly increased their longest recesses during two nesting attempts ($S1_a$ and S2, Fig. 4A, D). One female's ($S1_a$) longest recesses increased at a rate comparable to that of successful females until we confirmed the loss of her young (Fig. 4A). Her longest recesses then became erratic and were likely affected by our

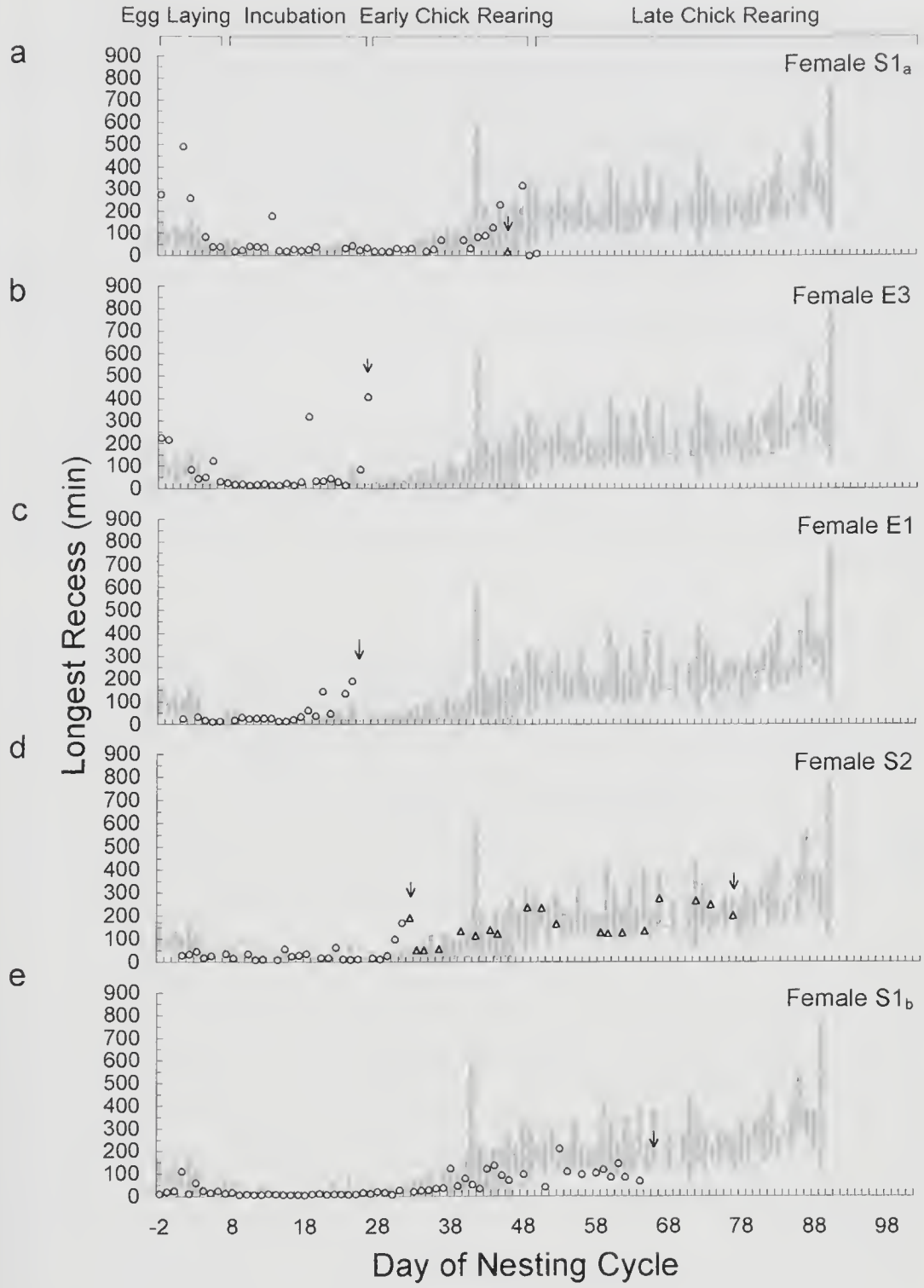

FIG. 4. Longest recesses (longest period out of nest) by female Puerto Rican Parrots during failed nesting attempts. Symbols are as given in Fig. 1.

attempts to foster surrogate young into her nest (Fig. 4A). During the S2 nesting attempt, the female showed an unexpected sharp increase in her longest recesses on day 30, two days before we confirmed loss of her young (Fig. 4D). Following successful fostering of surrogate young into her nest, however, this female resumed a pattern of longest recesses comparable to that of females that successfully fledged young (Fig. 4D).

During late chick rearing, the $S1_b$ female took only short recesses from her nest ($\bar{x}$ = 103.1 min ± 13.2 min SE). Females that successfully fledged young frequently left their nests for much longer periods (range of daily $\bar{x}$ = 144.3 min ± 12.1 min SE to 281.7 min ± 68.5 min SE) (Fig. 4E).

Male nest attendance and frequency of male nest entries.—During incubation, the E1 male often entered his nest more frequently and spent more time in his nest than did males that successfully fledged young. He entered his nest most frequently and maintained particularly high nest attendance during the four days before he abandoned his nest (Figs. 5A, 6A).

During early chick rearing, the $S1_a$ male failed to establish a regular pattern of at least one nest entry per day (Fig. 6B). Except for one incident (one male on one day, day 48), all successful males tended to enter their nests regularly after day 38 and most males established a regular pattern of daily visits before this time (Wilson et al. 1995). In addition, the $S1_a$ male, who generally entered his nest less than three times per day during early chick rearing, showed a sudden increase in nest entries on day 44, one day before we confirmed the deaths of his young (Fig. 6B).

During late chick rearing, one male's ($S1_b$) nest attendance and frequency of nest entries were notably different from the behavior of males that successfully fledged young (Figs. 5C, 6C). This male's nest attendance and frequency of nest entries had been comparable to those of successful males during early chick rearing; however, on days 48, 50, and 51, he did not enter his nest (Fig. 5C), whereas successful males entered their nests at least once per day during this same period. His nest attendance ($\bar{x}$ = 1.7% ± 0.6% SE) and frequency of nest entries tended to be low during the remainder of observation compared to nest attendance (range of daily $\bar{x}$ = 3.4% ± 0.6% SE to 6.2% ± 1.7% SE) and frequency of nest entries by males that successfully fledged young (Figs. 5C, 6C).

DISCUSSION

The most common behavioral aberrations among parrots that abandoned their nests during incubation were low nest attendance and long absences from the nest by adult females. The two females that abandoned nests during incubation exhibited decreased nest attendance, increasing

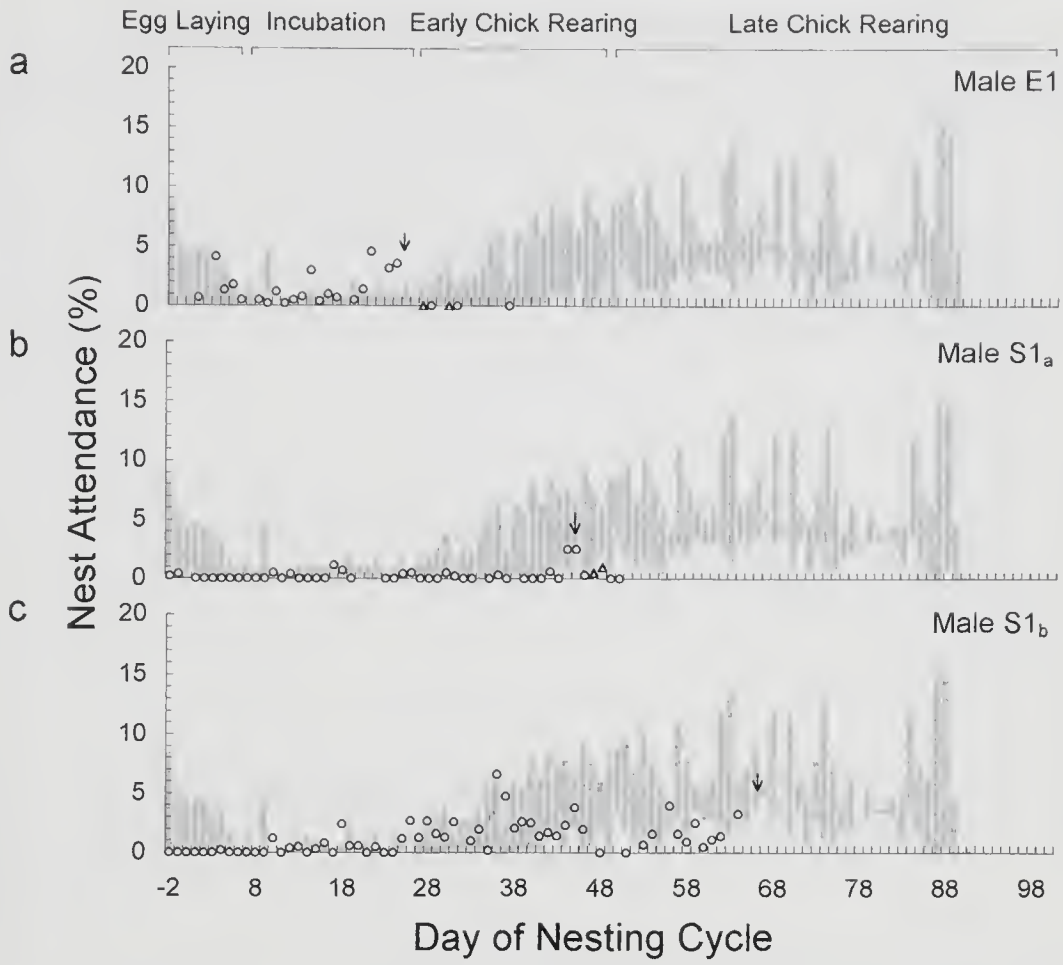

FIG. 5. Nest attendance (percentage of a 15-h period spent in nest cavity) by male Puerto Rican Parrots during failed nesting attempts. Note scale is different than scale used in Fig. 1, otherwise all symbols are the same.

mean recesses, and increasing longest recesses one to two days prior to abandonment. However, only one of two males that abandoned their nests exhibited differences in behavior prior to abandonment. The male began to spend more time in his nest and to enter his nest more frequently four days prior to abandoning his nesting attempt.

Females that lost their broods exhibited behavior similar to those that abandoned their nesting attempts during incubation. Females that lost their broods exhibited unexpected declines in nest attendance and either took longer recesses or entered their nests more frequently one to two days prior to our discovery of the loss of their young. Therefore, unexpected declines in female nest attendance accompanied by increases in the length of female recesses or in frequency of female nest entries may be the most reliable indicators of imminent nest abandonment resulting from a variety of causes. We also noted that parrots often give "whining"

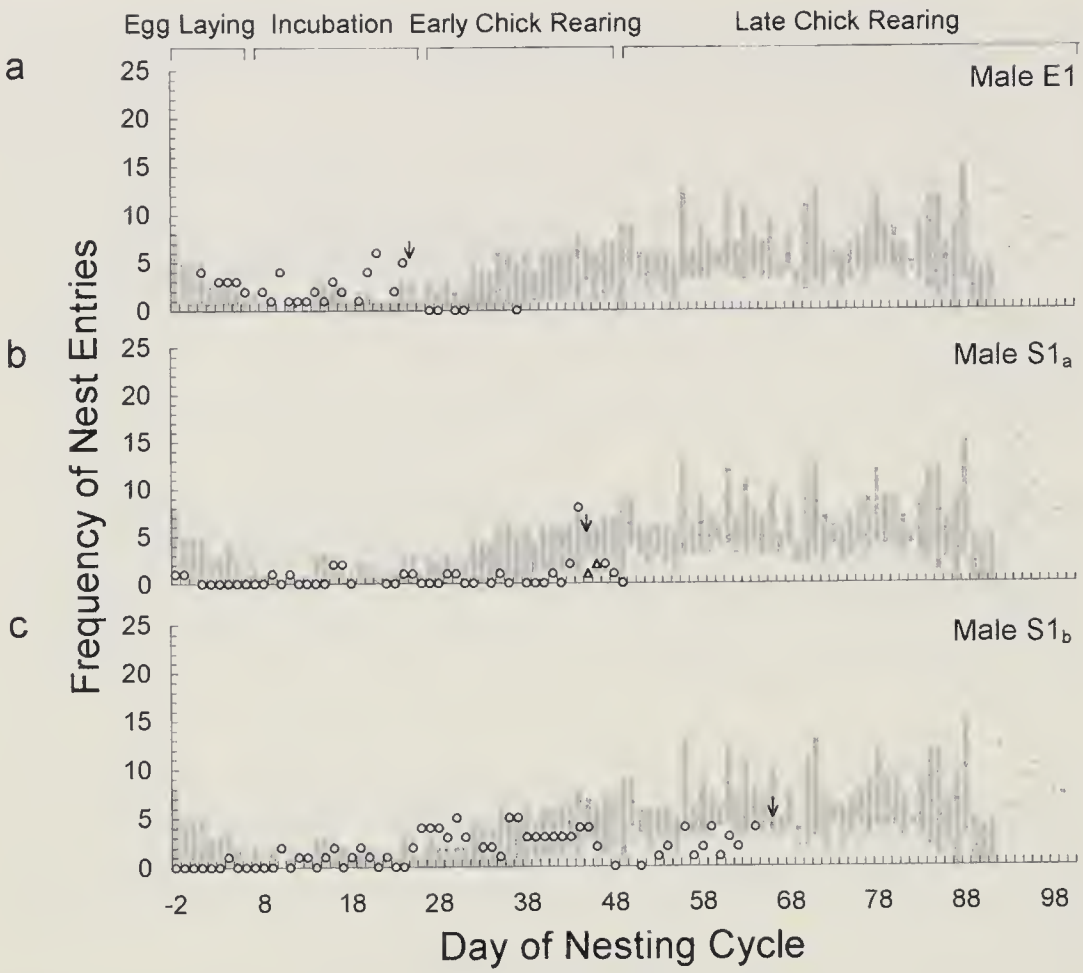

FIG. 6. Frequency of nest entries (number of visits per day) by male Puerto Rican Parrots during failed nesting attempts. All symbols are as given in Fig. 1.

or "wailing" vocalizations during "high anxiety" situations such as intense territorial defense, nest abandonment, and loss of a brood, but we did not have adequate data to determine if such vocalizations could be used as indicators of threats to reproductive success.

Although differences in the behavior of female parrots were clearly associated with nest failure during this study, whether such behavioral changes contributed to or caused the death of embryos and young is unknown. Well-developed embryos and older chicks can withstand cooling (Low 1987, Snyder et al. 1987, Jordan 1989); however, incidents of embryo chilling and low incubation temperatures in captivity can lead to embryonic mortality, hatching failure, or successful hatching of small, weak chicks and/or death of chicks at a young age (Low 1987, Van Der Heyden 1987, Jordan 1989, Kuehler and Good 1990, Stoodley and Stoodley 1990). Little is known about the effects of temperature variation on parrot embryos and young in wild nests. Embryos and/or young from three nesting attempts observed during this study (E1, E3, and $S1_a$) may

have been exposed to chilling by low nest attendance and/or long absences from the nest by females during incubation. However, these embryos also experienced other conditions that may have affected their survival. The E3 and E1 embryos, which were removed from the nests and completed incubation/hatching in captivity, may have been stressed or damaged by jarring experienced during transport from field to aviary (Kuehler and Good 1990, Stoodley and Stoodley 1990). The $S1_a$ brood had been mostly consumed by insect larvae by the time we inspected the nest; whether infestation occurred prior to (Snyder et al. 1987) or following death of the young is unknown.

Similarly, the pattern of chronically low frequency of nest entries exhibited by the $S1_a$ male during early chick rearing may have affected the survival of his young directly, may have resulted from the chicks' behavior, or may have been unrelated to failure of his nesting attempt. Because other males tended to enter their nests regularly to feed their young (Wilson et al. 1995; KAW and MHW, pers. obs.), a chronically low frequency of nest entries by males may indicate inadequate feeding of the young. If we assume that males are stimulated to enter their nests by vocalizations of the young, infrequent entries may also result from ailing chicks that beg less frequently or less vigorously. We do not have data to support or refute any of these explanations.

We believe that behaviors that appeared one to two days prior to our discovery of the loss of a brood (as opposed to those that occurred earlier in the nesting cycle) during this study were the result of the absence of stimuli ordinarily provided by healthy young rather than the proximate cause of the loss. Both pairs that lost a brood during early chick rearing ($S1_a$ and S2) had successfully raised several previous broods, and we observed no other circumstances that might have stimulated declining interest in a nest (e.g., disturbance, Wilson 1993, Wilson et al. 1995). Also, we have no other records of declining attentiveness by Puerto Rican Parrots without the presence of potential causes of such behavior.

Although behavior of the $S1_b$ pair was notably different throughout late chick rearing than that of pairs that successfully fledged young, we believe their behavior was unrelated to the loss of their brood. The oldest chick, which appeared to have beak and neck abnormalities and poor growth, died at approximately 15 days of age (i.e., during early chick rearing) from unknown causes. The remaining chick died on day 66 after exhibiting symptoms of the "growth syndrome" that afflicted one chick of each brood from this nest during all four years of the study period. Typical symptoms of the syndrome include suspended weight gain at 180 g, poor feather growth, susceptibility to infection and ultimately death in spite of intensive veterinary care. Given the nature and incidence of the

illness, the syndrome may be of genetic origin. Behavior of the pair may have been related to scarcity of Sierra palm (*Prestoea montana*) fruit, the parrots' primary food source during the breeding season (Snyder et al. 1987), caused by almost complete defoliation of vegetation during Hurricane Hugo in September of 1989. However, another pair nesting in a different valley successfully raised three young later that same season.

A likely explanation for the high attendance by the $S1_b$ female and infrequent nest visits by the $S1_b$ male during late chick rearing is small brood size (1 young). Snyder et al. (1987) found that females with a single chick tended to maintain high nest attendance later in the nesting cycle than did females with larger broods. During our study, we observed such consistently high female nest attendance during late chick rearing during only one other nesting attempt (a successful attempt, Wilson et al. 1995) which also contained only one chick during the first part of the late chick rearing stage. Similarly, the $S1_b$ male exhibited behavior like that of the male of the successful nesting attempt noted above. On days 48, 50, and 51, the $S1_b$ male did not enter his nest, whereas he had previously entered his nest one to six times per day. The successful male also suddenly failed to enter his nest on day 48. Although other factors might affect a male parrot's attentiveness (Wilson 1993, Wilson et al. 1995), we observed no change in levels of conspecific activity, human activity, or vocalizations by the chick prior to or during the $S1_b$ male's decline in nest attendance.

Although the implications of these results are limited by small sample size, this study provides an initial detailed description of Puerto Rican Parrot reproductive behavior during failed nesting attempts. Observers should now be able to identify behavior indicative of nest problems and take appropriate management action. Upon recognition of these behaviors, biologists can remove eggs or chicks from nests threatened by abandonment and replace them with artificial eggs or surrogate young until the behavior of the pair returns to acceptable levels. Ill or injured young can be removed from nests for treatment and replaced with young of a surrogate species or with other Puerto Rican Parrot young. Even if biologists are unable to prevent deaths of embryos and young, maintenance of nesting activity by fostering may prevent pairs from adopting different and perhaps less suitable nest sites the following season (Wiley 1983).

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OVERLAND TRAVEL, FOOD ABUNDANCE, AND WETLAND USE BY MALLARDS: RELATIONSHIPS WITH OFFSPRING SURVIVAL

E. H. Dzus[1,2,3] and R. G. Clark[1,2]

Abstract.—We monitored wetland habitat use and inter-wetland moves of 52 Mallard (*Anas platyrhynchos*) broods near Yorkton, Saskatchewan. Brood-attending females were equipped with radio transmitters and their locations monitored daily. Duckling survival in the first two weeks after hatching was not related to distance traveled to the first wetland nor the total distance traveled overland in the 14-day period. Brood-rearing females were found on one to five wetlands in the first week after hatch (mode = 2), and most (17 of 32) remained on one wetland in the second week (range = 1–5). Broods were found most frequently (69–95% of days) on semi-permanent wetlands. Conductivity on most (>95%) of these wetlands was <2000 microsiemens/cm; such levels are well below those known to affect duckling growth or survival. For 12 broods for which we had data on food (chironomid) abundance, we were unable to detect a relationship between inter-wetland movements and brood use. Nor was there evidence that duckling survival was related to levels of chironomid abundance. *Received 3 Sept. 1996, accepted 20 Feb. 1997.*

Mallard broods typically use several wetlands during the brood-rearing period, but causes and consequences of these moves remain unresolved. Early studies of wetland use by Mallards (*Anas platyrhynchos*) relied on observational brood surveys (e.g., Berg 1956, Mack and Flake 1980, Monda and Ratti 1988, Mulhern et al. 1985). However, the secretive nature of brood-rearing females makes conclusions based on data collected from radio-marked birds more complete. The brood-rearing period for most dabbling ducks remains the least understood component of their annual cycle, despite the fact that natural mortality from hatching to fledging is higher than in later life stages (e.g., Johnson et al. 1992, Rotella and Ratti 1992a). Hence, evaluating factors that influence overland movements and wetland habitat use during the brood-rearing period, and their effects on survival, is crucial for a thorough understanding of waterfowl population dynamics.

Studies examining the impact of overland movements have yielded conflicting results. Two studies suggested that long overland moves reduced survival of Mallard ducklings (Ball et al. 1975, Rotella and Ratti 1992b), whereas Talent et al. (1983) did not find support for this hypoth-

[1] Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2 Canada.
[2] Canadian Wildlife Service, 115 Perimeter Rd., Saskatoon, Saskatchewan S7N 0X4, Canada.
[3] Present address: Dept. of Biological Sciences, CW405 Biological Sciences Building, Univ. of Alberta, Edmonton, Alberta T6G 2E9, Canada.

esis. Thus, further information is needed to evaluate whether offspring survival is related to overland movements.

Wetland use could be influenced by a variety of factors, including wetland conditions (vegetation characteristics and permanency of aboveground water) or water chemistry. Salinity of wetlands may affect habitat use, as it is known to negatively affect duckling growth and survival (Mitcham and Wobeser 1988, Swanson et al. 1984). Effects of wetland characteristics may act directly on duckling survival or indirectly through effects on predation risk and food availability.

Food abundance may also play a role in wetland selection by brood-rearing females. Dipterans, primarily of the family Chironomidae, are the most commonly reported animal food of young Mallard ducklings (Chura 1961, Sugden 1973, Krapu and Swanson 1977, Street 1977). Emergence patterns of chironomids typically show early summer peaks (e.g., Rasmussen 1984, Wrubleski and Rosenberg 1990), and diversity of the invertebrate fauna is related to wetland vegetation characteristics and water permanency (Driver 1977).

Our objectives were to (1) evaluate overland brood movements of Mallards and relate these moves to survival of ducklings and (2) examine wetland use by Mallard broods in terms of wetland type, water chemistry and food availability.

STUDY AREA AND METHODS

We conducted the study 40 km west of Yorkton (51°12′N, 103°7′W) in east-central Saskatchewan, Canada, from 1990 to 1993. The area consisted of five managed waterfowl nesting areas (63 ha each) that lie in the aspen parkland zone of the prairie pothole region of North America. The region is characterized by gently undulating topography, interspersed with aspen (*Populus tremuloides*) bluffs and has a moderate wetland density (range in mid-May, 27 to 49/km^2). The primary land use in the region consists of cereal and oilseed crop production.

The number of wetland basins holding water was counted during weekly waterfowl surveys from early May until mid July. Wetlands were classified according to Stewart and Kantrud (1971). Class IV (semi-permanent) and class V (permanent) wetlands were grouped together and are referred to as semi-permanent wetlands. Class I (ephemeral), Class II (temporary), and Class III (seasonal) wetlands formed the second wetland category (hereafter referred to as seasonal wetlands). Most Class I and II wetlands were dry by the time broods appeared. Conductivity was measured in July each year using a hand-held conductivity meter. One reading was taken in shallow emergent, deep emergent, and open water zones; the average was taken as the measurement for the wetland.

Mallard nests were found by searching on foot or using cable-chain drags pulled between two all-terrain vehicles (Klett et al. 1986). Because nesting success of ducks in the prairie pothole region is so low (Greenwood et al. 1995), we protected nests with fences. Mallard nests that were not located in one of two 16-ha predator exclosure fences (Trottier et al. 1994) were surrounded by wire mesh fences if they survived to late egg-laying or early incubation stays (Sargeant et al. 1974, Greenwood et al. 1990). Females were captured at

about day 20 of incubation using hand-carried mist nests (Bacon and Evrard 1990) or automatic walk-in nest traps (Weller 1957). All females received leg bands, unique combinations of nylon nasal markers (Lokemoen and Sharp 1985), and radio transmitters. All females in 1990, half of the females in 1991, and one female in 1992 received 22-g harness-style transmitters (28 × 18 × 8 mm, model CHP2H, Telonics Inc., Mesa, Arizona, USA) using a criss-cross modification (Smith and Gilbert 1981) of the traditional Dwyer (1972) harness. The remaining brood-rearing females in 1991 and 1992, and all individuals in 1993, had a 21-g cylindrical transmitter (23 mm diam. × 53 mm, model IMP150, Telonics Inc.) implanted into their abdominal cavity (Olsen et al. 1992). Females were placed back on nests in a mild, methoxyflurane-induced state of anesthesia to reduce nest abandonment (Smith et al. 1980, Rotella and Ratti 1990). The use of different types of transmitters does not bias results presented here because offspring survival was not influenced by transmitter-type carried by the female (Dzus and Clark 1996).

Females were located one to four times daily, using either a truck-mounted or hand-held receiving system (White and Garrott 1990:47–75), and locations were plotted on aerial photomaps. Distances from nest to the first wetland used and inter-wetland distances were measured on photomaps (to the nearest 10 m). As the actual travel path of the brood was not known, we recorded linear distances. Logistic regression (PROC CATMOD, SAS Inst. Inc. 1990) was used to determine if brood fate at 14 days after hatching (response variable) was influenced by distance to the first wetland used. CATMOD was used because we had to control for annual differences and seasonal changes in nest to wetland distances, and to test for interactions among predictor variables: year, hatching date, and distance traveled (note: these variables were *not* divided into categories).

Observations to determine brood size were conducted at least every seven days after hatching until the young could fly (approximately 55 days, Bellrose 1976). Estimates of offspring survival were based on visual observations of broods attended by radio-marked females. Duckling survival (i.e., attrition within a brood) was calculated for each brood using a modified Mayfield technique (Flint et al. 1995). Brood survival estimates represent ≥1 ducklings surviving to 14 d. Because individual ducklings were not radio-marked, we could not determine causes of mortality. We restricted all survival analyses to the first two weeks after hatching because (1) it allowed us to maximize our sample of broods and because (2) duckling mortality is greatest in the first two weeks after hatching (e.g., Ringelman and Longcore 1982, Orthmeyer and Ball 1990).

Brood size was manipulated to ±50% of modal size from 1991 to 1993 as part of another study (Dzus and Clark 1997). Brood survival was lower for reduced broods ($P < 0.05$) but did not differ between control and enlarged broods ($P = 1.0$, Dzus and Clark 1997). Therefore, for analyses using brood fate, reduced broods were excluded, and data for control and enlarged broods were combined. Duckling survival in reduced and enlarged broods tended to be lower than control broods (Dzus and Clark 1997); therefore, analyses using individual duckling survival include only control broods.

We sampled aquatic invertebrates during the first two weeks after hatching using 1-m^2 emergence traps for a subsample of Mallard broods from 1991 to 1993 (Ross and Murkin 1989). Because of a limited number of emergence traps, broods could be included for invertebrate sampling only when traps became available. There is no reason to believe a bias existed in our selection of broods for invertebrate sampling, nor was there any indication of effects on brood movements from the placement of traps. The first 14 days were sampled because most duckling mortality occurs in this period (e.g., Orthmeyer and Ball 1990, Ringelman and Longcore 1982) and because young ducklings feed extensively on emerging invertebrates (Pehrsson 1979). Two traps were placed at randomly selected locations on wetlands used by broods; one trap was placed in emergent vegetation and the other in open

water one day after the brood arrived on the wetland. If one of the two zones was missing in a wetland, both traps were placed at random in the existing zone. If the brood moved, additional traps were placed on the new wetland. Samples were collected every seven days, stored in 70% alcohol and later sorted into chironomids and "others." Chironomids were classified by size class and subfamily: Chironominae (small, medium and large), Tanypodinae (medium), and Orthocladinae (small) and biomass conversions followed Lapointe (1986). We evaluated whether broods moved to wetlands with higher chironomid biomass by comparing chironomid biomass (log X + 1) of the first wetland used to the last wetland used in the first two weeks of duckling life, using the Wilcoxon signed-rank test. We also compared chironomid availability between wetlands used by females that had young and those experiencing total brood loss using a Wilcoxon-Mann-Whitney test; chironomid biomass/wetland was weighted by the number of days the brood spent on the pond, and a weighted mean biomass was calculated for each brood.

All research methods employed during our study were approved by the Animal Care Committee, Univ. of Saskatchewan, on behalf of the Canadian Council on Animal Care.

RESULTS

Wetland density and initial nest-to-wetland moves.—There were substantial differences in wetland density between years, with 1990 having the greatest wetland abundance and 1993 initially having the lowest density until early summer rains refilled many dry wetlands (Fig. 1). Distances from Mallard nests to the closest wetland (regardless of permanency of water) and the closest semi-permanent wetland were significantly greater ($P = 0.05$, Bonferonni t-test) in 1993 than in 1990 and 1991 when wetlands were more abundant (Table 1).

Only 19 of 52 (37%) brood-rearing females moved from their nest to the closest wetland with standing water. The average distance from the nest to the first pond used was 211 m (N = 26, SD = 183) for broods surviving to 14 d and 310 m (N = 9, SD = 206) for broods experiencing loss of all ducklings (note: experimentally reduced broods excluded). Brood survival was not related to distance moved to the first wetland (logistic regression, $\chi^2 = 1.58$, df = 1, $P = 0.21$, two- and three-way interactions with year and relative hatching date were not significant, $P > 0.05$, and were removed from the model; Likelihood ratio: $\chi^2 = 34.3$, df = 29, $P = 0.23$).

Brood movements.—Of 40 Mallard broods for which we have reliable movement data (experimentally reduced broods excluded), most made two (N = 14) or three (N = 10) moves in the first seven days after hatching (range = 1–5). Sample size was too small to evaluate reliably survival consequences in relation to number of moves. Most (17 of 32) Mallard broods were sedentary in the second week after hatching, while other broods made one (N = 6), two (N = 4), three (N = 2), or five (N = 3) moves in the second week. For broods that fledged young (N = 21), there was a large degree of variability in the number of moves re-

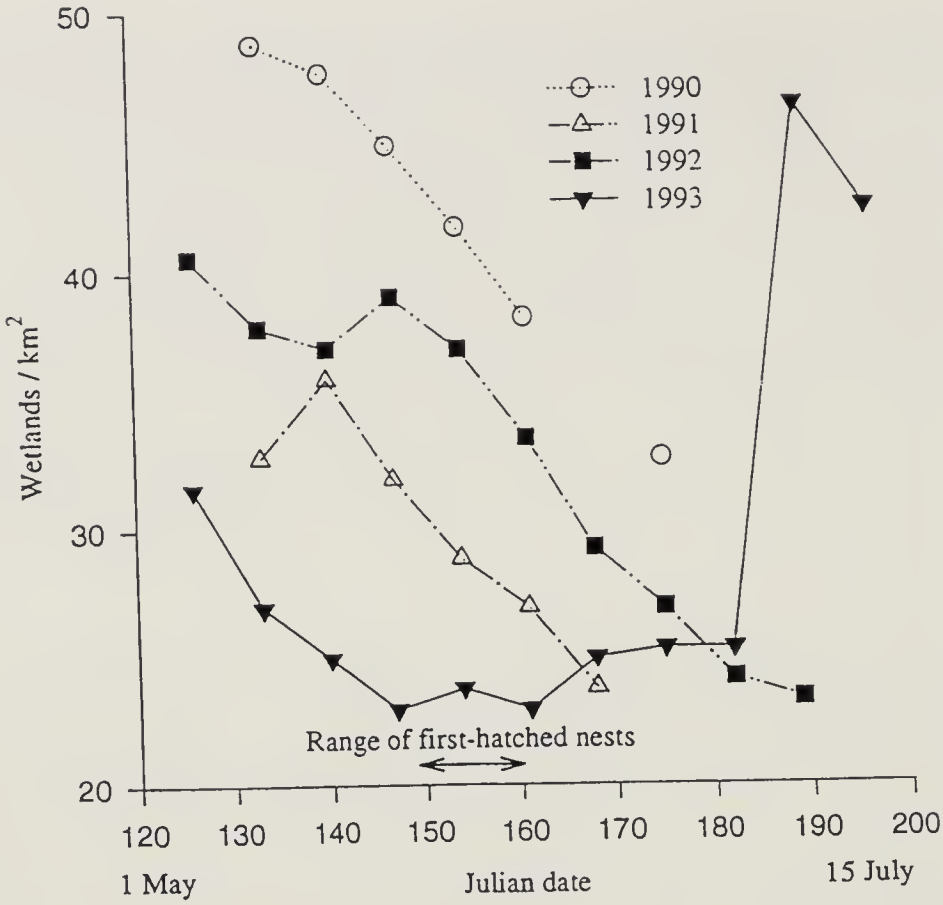

FIG. 1. Wetland density on managed nesting areas near Yorkton, SK, from 1990 to 1993.

TABLE 1

ANNUAL VARIATION IN DISTANCES (m) FROM MALLARD NESTS TO THE CLOSEST WETLAND WITH STANDING WATER AND CLOSEST SEMI-PERMANENT WETLAND, FROM 1990 TO 1993 NEAR YORKTON, SASKATCHEWAN

		Closest wetland[a]		Closest semi-permanent wetland	
Year	Broods	$\bar{X}$[b]	SD	$\bar{X}$	SD
1990	16	75A	59	103A	93
1991	15	78AB	36	102A	53
1992	11	131BC	54	135AB	62
1993	11	183C	60	190B	54
F		11.83		4.36	
P		0.0001		0.008	

[a] Closest wetland refers to a wetland basin with standing water, regardless of permanency.
[b] Means with the same letter are not significantly different (Bonferonni *t*-test, $P = 0.05$).

corded during the period from 15 to 30 days after hatching. Six broods remained on the same wetland, four moved once, and the remainder (N = 11) made between three and 12 moves in this latter period.

Total distance traveled overland was similar (Wilcoxon 2-sample test, $P = 0.58$) between broods that had at least one duckling survive to 14 days (N = 26, median = 893 m) and those that did not (N = 9, median = 870 m). Similarly, duckling survival did not vary with total distance traveled (Spearman rank correlation, $r_s = -0.23$, N = 27, $P = 0.12$). A one-tailed test was used based on a predicted inverse relationship between duckling survival and distance traveled overland (Ball et al. 1975, Rotella and Ratti 1992b).

Brood use of wetlands as a function of wetland characteristics.—In all years of the study, broods used semi-permanent wetlands most frequently (69–95% of brood-days). Broods that fledged young seemed to spend more days in weeks 1 and 2 on semi-permanent wetlands than females that experienced total brood loss (Fig. 2). However, when examined on a per brood basis, there was no relationship between duckling survival and percent of days located on semi-permanent wetlands ($r_s = 0.20$, N = 27, $P = 0.29$, two-tailed).

Broods (N = 37) spent the majority of their time on wetlands with conductivity <2000 microsiemens (μS)/cm. Only seven of 247 (2.8%) brood-days in week 1 and 18 of 215 (8.4%) brood-days in week 2 were spent on wetlands with conductivity >2000 μS/cm, and the maximum conductivity recorded for a wetland used by a Mallard brood was 3633 μS/cm. On our study area, the highest value recorded was 3800 μS, and few wetlands had values greater than 2000 μS/cm.

There was no trend for the last wetland used by broods to have higher chironomid biomass than the first-used wetland (emergent and open-water samples combined) (Wilcoxon signed ranks test, $T^+ = 36$, $P = 0.43$, one-tailed test); this held true whether we used emergent ($T^+ = 44$, N = 11 broods, $P = 0.18$) or open-water samples ($T^+ = 32$, N = 10, $P = 0.35$). Furthermore, mean biomass of chironomids (weighted by the number of days the brood spent on the wetland) did not differ between wetlands used by broods with young surviving after 14 days and those that did not (Wilcoxon-Mann-Whitney test, m = 5, N = 6, Wx = 31, $P = 0.60$, Table 2).

DISCUSSION

Some previous studies have found a negative relationship between distance traveled overland and duckling survival (Ball et al. 1975, Rotella and Ratti 1992b). However, Talent et al. (1983) and this study did not detect a relationship between distance traveled and offspring survival. Differences between these studies may relate to wetland density, food

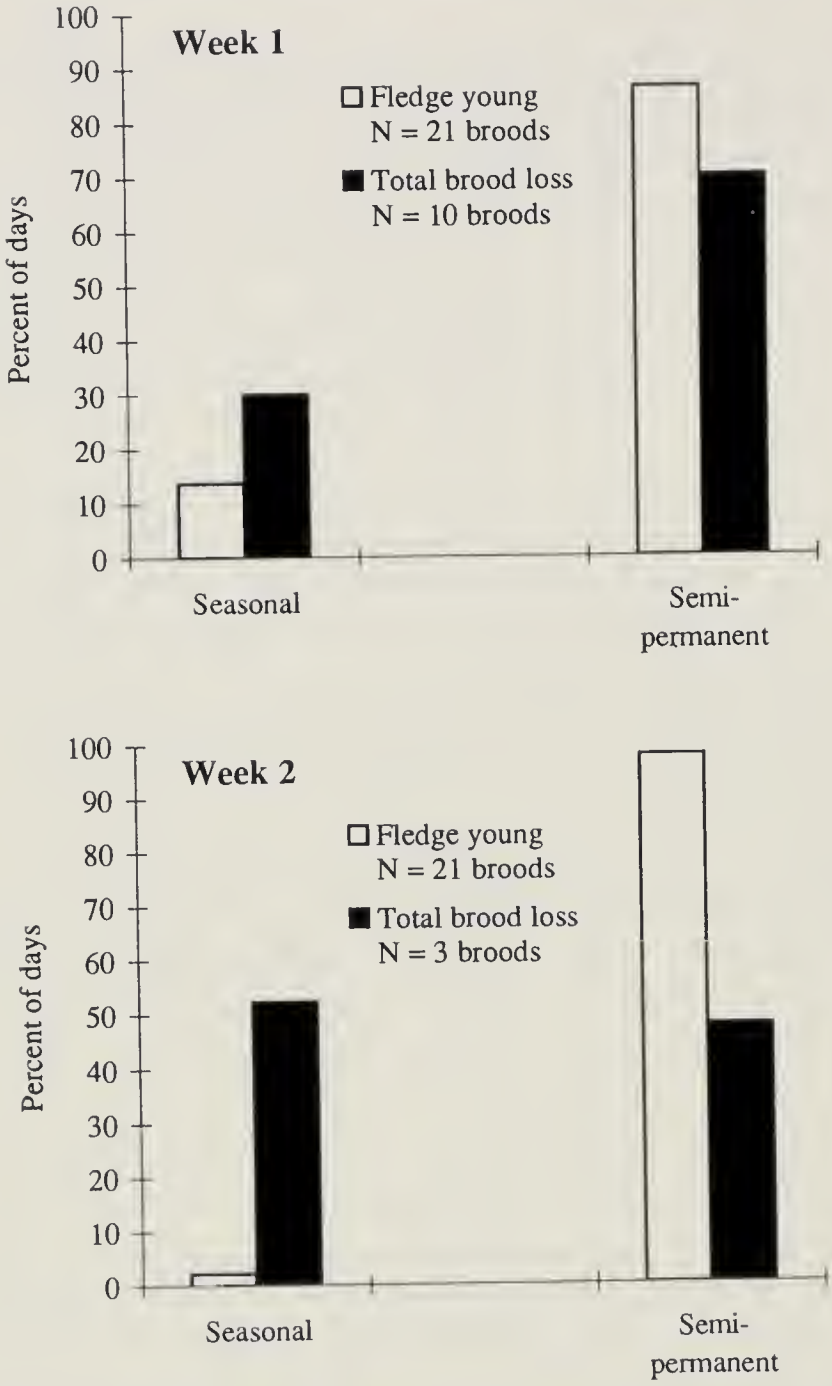

FIG. 2. Fate of Mallard broods in relation to wetland classification near Yorkton, SK, from 1990 to 1993.

availability, weather conditions, predator populations, or other factors. Wetland density on Rotella and Ratti's (1992b) study area ($\bar{x}$ = 11/km^2, range 0 to 32/km^2) was much less than our study (see Fig. 1), but greater than that of Talent et al. (1983: range 2–14/km^2). Rotella and Ratti (1992b) presented movement data for a 30-d period; if calculated for a

TABLE 2

CHIRONOMID BIOMASS IN WETLANDS USED BY BROODS THAT HAD YOUNG SURVIVING PAST 14 DAYS AFTER HATCHING AND THOSE THAT DID NOT (YORKTON, SASKATCHEWAN, 1991 TO 1993)

Brood fate Brood[b]	Number of wetlands used in first 14 d	Chironomid biomass[a]		
		First wetland[c]	Last wetland[c]	Mean[d]
Total brood loss by 14 days:				
2420/91	4	3.49	2.94	3.41
3260/91	3	8.72	11.15	8.94
2050/93	4	9.47	5.36	5.61
2070/93	3	9.11	8.22	8.48
2580/93	2	8.22	10.18	9.98
Duckling(s) survive > 14 days:				
3240/91	4	8.03	8.87	7.30
2620/92	3	7.86	9.19	8.35
2780/92	2	9.22	7.49	7.61
3200/92	5	5.68	5.10	4.79
3230/92	4	8.97	8.06	8.05
2030/93	2	5.38	12.64	12.12

[a] Calculated as the sum of the emergence and open water traps per seven-day sampling period, expressed as ln (mg/m^2/week).
[b] Identified by radio frequency and year.
[c] First and last wetland used in the 14 days after hatching.
[d] Mean chironomid biomass per wetland weighted by the number of days spent on the wetland.

14-d period, based on average distance moved per day, their broods would have moved 1204 m compared to an average of 875 m in our study. It is possible that there is some threshold of risk where distance traveled overland becomes a significant factor influencing mortality. Six of eight broods in our study that traveled >1200 m in 14 d had duckling survival probabilities lower than average. Whether such a relationship is related to wetland density is questionable. Talent et al (1983) suggested that brood movements and duckling survival may have been related to the presence or absence of mink on a particular wetland. Mink were not likely an important predator on our study area because their primary prey, muskrats, were not found on wetlands during our study (E. Dzus, pers. obs.). As such, without detailed information on movement and mortality events derived from radio-marked ducklings, discussion of the risks of overland travel will remain speculative.

Mallards consistently showed high use of semi-permanent wetlands, despite changing wetland conditions over the four years of study. Temporary wetlands were available to Mallards, especially in the wettest year (1990), yet brood-rearing females showed little use of these wetlands. Rotella and Ratti (1992b) studied Mallard brood habitat use in dry years in southwestern Manitoba and reported high use of semi-permanent wet-

lands. Preference for seasonal wetlands that exhibit extensive coverage of emergent vegetation was reported by Talent et al. (1982) and Mauser et al. (1994b). Thus, there appears to be geographic variability in wetland use by Mallard broods.

Little information is available relating brood use of wetlands to wetland conductivity. Most prairie wetlands have conductivity <4000 μS/cm (Leighton and Wobeser 1994). The vast majority of wetlands used by Mallard broods in this study had very low conductivity values (<2000 μS/cm). Such levels were well below those shown to be fatal to young ducklings (>20,000 μS/cm) or known to affect growth (Mitcham and Wobeser 1988, Swanson et al. 1984). Conductivity did not affect selection of wetlands by brood-rearing American Black Duck (*A. rubripes*) females (Ringelman and Longcore 1982). Thus, wetland conductivity was unlikely to have had any effects on duckling growth or survival on our study area.

Food abundance may be an important, yet poorly-quantified, factor influencing wetland use. We found no relationship between the abundance of emerging chironomids and duckling survival. Talent et al. (1982) found some support for the hypothesis that brood-rearing females move to wetlands with higher chironomid abundance. A potential problem exists with the study of Talent et al. (1982); they sampled larval chironomids in the benthos, which may not necessarily reflect availability of emerging adults to young ducklings at or near the time of sampling. Talent et al. (1982) further suggested that seasonal wetlands support higher densities of benthic invertebrates (based on the work of Swanson and Meyer 1973). Contrary to this, Nelson (1989) found that semi-permanent wetlands supported higher densities of chironomid larvae than seasonal wetlands. Limited heterogeneity in plant species diversity and vegetation structure, in combination with total loss of surface water and low nutrient status, may operate in concert to limit the development of complex chironomid communities in seasonal wetlands (Driver 1977, Driver and Peden 1977, Wiggins et al. 1980). Thus it is not clear what the role of food is in influencing wetland movements of Mallard broods.

The period from hatching to fledging remains the least understood period of the Mallard's life cycle. To further our understanding of brood ecology, it will be necessary to study intensively individually radio-marked ducklings. However, before we begin examining the factors influencing duckling survival, we must be convinced by experimental studies with appropriate controls that there is no negative impact of the marking technique on such small animals. Once techniques have been refined, we can begin to examine relationships between invertebrates, habitat use by broods, age of female, hatching date, duckling survival, and causes of mortality in a comprehensive study with a large sample of broods.

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SHORT COMMUNICATIONS

Acquisition and recall of Gambel's Sparrow dialects by Nuttall's White-crowned Sparrows in the wild.—Three subspecies of White-crowned Sparrow (*Zonotrichia leucophrys*) occur in the San Francisco Bay Area of California. Nuttall's Sparrow (*Z. l. nuttalli*) is a circumannual resident (Blanchard 1941, DeWolfe et al. 1989) and often encounters the migratory Puget Sound Sparrow (*Z. l. pugetensis*) which breeds from northern California to British Columbia and winters in the San Francisco Bay Area (Blanchard 1941; DeWolfe and Baptista 1995). The boreal Gambel's Sparrow (*Z. l. gambelii*) also overwinters in the San Francisco Bay Area (Blanchard and Erickson 1949:259). However, in many years of intense banding during migration, DeWolfe (pers. comm.) found that only about 1% of wintering migrant flocks consisted of *gambelii*. The rest were mostly *pugetensis*.

Since 1968, Baptista has encountered twelve territorial White-crowned Sparrows in the San Francisco Bay Area singing songs typical of Puget Sound Sparrows. Ten were positively identified as Nuttall's Sparrows (Baptista 1974, Baptista 1977, and unpubl. data). Nuttall's Sparrows may learn Gambel's Sparrows songs in the laboratory (Baptista and Petrinovich 1986), yet learning of Gambel's Sparrow songs by Nuttall's Sparrows has not been encountered in the wild. We document herein two incidences of Nuttall's Sparrows learning Gambel's Sparrow songs in the wild, and postulate how they acquired these songs.

At 08:15 on 15 May 1993, Baptista heard a song typical of a migratory Gambel's Sparrow (Fig. 1A) on the corner of Pacheco and Sunset Boulevard, San Francisco, California. On 27 May, we recorded an individual (probably the same one) singing a Gambel's Sparrow song (Fig. 1B) as well as a Nuttall's Sparrow theme at this same locality (Fig. 1D, E). This individual (henceforth referred to as G1) responded to playback with approach, aggressive trilling, song, and display, suggesting that he was defending a territory. On 18–19 June 1996, we recorded a second individual (G2) singing a song typical of wintering Gambel's Sparrows (Fig. 1C) in Golden Gate Park, San Francisco, and this bird also responded to playback, indicating that it had settled on a territory. Subsequently, both G1 and G2 were trapped, color-banded and identified to subspecies (see below).

Songs of Gambel's Sparrows are easily distinguished from those of Nuttall's Sparrows from San Francisco on the basis of syllable structure and syntax (Austen and Handford 1991; Baptista and King 1980; Chilton et al. 1990; Chilton and Lein 1996a; DeWolfe et al. 1974; Kern and King 1972). We recorded 27 renditions of Gambel's songs and eight renditions of Nuttall's songs from G1 on May 27 and examined them with a Kay Elemetrics DSP continuous Spectral Analyser. Songs of four Nuttall's Sparrow neighbors were also recorded for comparison. Six of G1's Gambel's songs ranged in duration from 2.06 to 2.20 sec ($\bar{x}$ = 2.13 sec). The warble following G1's introductory whistle (Fig. 1B) was similar to warble number six from DeWolfe et al.'s (1974) catalogue. Other than variation in duration his songs were very stereotyped and typical of those described by DeWolfe et al. (1974) for Gambel's Sparrows.

Ten of G2's songs ranged from 2.1 to 2.34 sec ($\bar{x}$ = 2.26 sec) in duration. The warble following the introductory whistle in G2's song (Fig. 1C) may also be assigned to type six in DeWolfe et al.'s (1974) catalog. The two buzzes that follow the warble are typical of Gambel's songs (compare with A), however, the terminal trill does not match any Gambel's song published to date. Terminal buzzes range from about 2.5 or 2.75 to 6 kHz, and this is always preceded by a syllable ranging from about 3 or 3.5 kHz to 7 or 7.5 kHz. The structure of each syllable in G2's terminal trill and the fact that they range from 3 to 7.5 kHz suggests

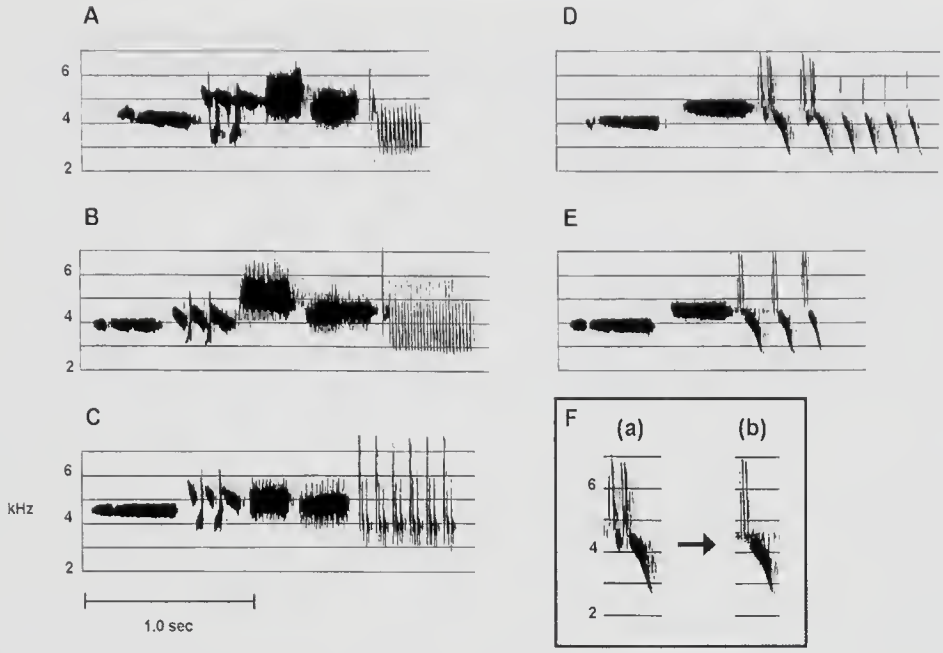

FIG. 1. (A) Gambel's Sparrow song from a visiting territorial migrant recorded on 20 December 1993. (B) Gambel's Sparrow song of bird G1. (C) Gambel's Sparrow song of bird G2. (D) Nuttall's Sparrow theme of neighbor of G1. (E) Nuttall's Sparrow theme of G1. (F) (a) Complex syllable of song D. (F) (b) Trill syllable from song E. Note that this is the second subsyllable of complex syllable (a).

that G2 improvised during song ontogeny and constructed a novel trill consisting of syllables typically preceding the terminal buzz in Gambel's Sparrow songs.

G1 sang a second theme (Fig. 1E) similar to those of local Nuttall's White-crowned Sparrows (Fig. 1D). Following two introductory whistles, G1's renditions of a Nuttall's theme (Fig. 1E) contained three syllables which were a modification of the complex syllables in its immediate neighbor's song. G1's songs contain the second subsyllable of his neighbor's complex syllable type (Fig. 1D and insert F). Similar modifications of complex syllables are commonplace in songs of female Nuttall's Sparrows (Baptista et al. 1993a), but this is only the second time we have encountered this phenomenon in male song.

There is individual variation in complex syllables contained in Nuttall's songs (Baptista 1975, Petrinovich 1988). Four other Nuttall males were recorded near G1's territory, but only his immediate neighbor (Fig. 1D) sang a song containing complex syllables most similar to his. On 6 August 1993, Baptista returned to this locality and with playback attracted G1 and a second individual believed to be his mate. The two birds foraged within a meter of each other, no aggression was observed, and both birds arrived and left together. On this day G1 sang only Nuttall's songs.

To test if the unused song could be elicited by playback, Baptista played 101 Gambel's songs to G1 on 7 August 1993. G1 responded by approach, aggressive displays, and countersinging with the tape recorder. He sang 163 Nuttall's songs and only three Gambel's songs in response to playback. The first Gambel's song was sung only after 75 Gambel's songs were played to him. His preference had shifted from singing Gambel's songs to singing Nuttall's songs. The following year, on 27 May 1994, we played 78 renditions of his Gambel's songs, and he responded with 120 Nuttall's songs and four Gambel's songs. He had been singing only Nuttall's songs prior to our playback experiments.

Migratory Gambel's Sparrows are 100% separable from sedentary Nuttall's Sparrows in morphology (Blanchard and Erickson 1949). G1 and G2 matched the local Nuttall Sparrows in all the characteristics outlined by Blanchard and Erickson (1949) and Banks (1964). We conclude from this that G1 and G2 were local Nuttall's Sparrows that had acquired their song from migratory Gambel's Sparrows. How were the alien dialects acquired?

Gambel's Sparrows typically arrive on their wintering grounds between mid-September and early October and leave in mid- to late April. Blanchard and Erickson (1949) documented much singing, pursuits, and brief fights by newly arrived Gambel's Sparrows in September. Singing is sporadic throughout much of the winter and then increases over the winter level by the second week of March, notably when birds gather in their roosting tree (DeWolfe, pers. comm.). Nuttall's Sparrows have been seen feeding young from late March to early September (DeSante and Baptista 1989). Thus, early or late-hatched Nuttall's Sparrows could encounter overwintering Gambel's Sparrows in their acoustic environment.

We found, moreover, that an over-wintering Gambel's Sparrow would respond to playback of Nuttall's song with approach to the speaker, posturing, and loud singing (Fig. 1A). This individual was captured in Golden Gate Park, and banded and reappeared at the same site the following year. This suggests that not only do over-wintering flocks occupy exclusive home ranges (Mewaldt 1964) but that these areas may be defended with song even against allosubspecific individuals. Some juvenile Nuttall's Sparrows begin staking out territories and sing full songs between mid July and late September (DeWolfe et al. 1989, Baptista and Gaunt 1997). Such juveniles may challenge and countersing with visiting Gambel's Sparrows, and thus acquire the latter's song.

If Nuttall's Sparrows are able to acquire songs from visiting migrants and songs are passed on by vocal tradition, why are there not more individuals singing alien dialects and how are local song dialects preserved? Although individuals in the wild typically sing only one song type (more rarely two or three; reviews in Baptista and King 1980; Chilton and Lein 1996b), birds in the laboratory may be tutored with as many as seven dialects, elements of which may be produced during the rehearsed song stage (Marler and Nelson 1993). Marler and Nelson (1993) suggested that through the process of matched countersinging, the songs sung by a neighbor or neighbors are evoked and retained and those not present in the repertoire of local birds fall into disuse and are eliminated. There is thus "overproduction" during the practice stage, followed by narrowing of the repertoire as a result of social interaction.

Matched countersinging in the wild has been documented for several subspecies of White-crowned Sparrows (Baptista 1975, 1977; Baptista and Morton 1988; Chilton and Lein 1996b), and Baptista and Morton (1988) have documented narrowing of repertoire at the start of the first breeding season in the montane White-crowned Sparrow (*Z. l. oriantha*).

On 27 and 29 May 1993, G1's song repertoire consisted mostly of Gambel's songs (27 vs. 8 Nuttall's songs recorded). On August 6 and 7, his repertoire consisted mostly of Nuttall's songs (163 vs 3). Matched-countersinging with his three Nuttall's neighbors had apparently shifted his preference from singing Gambel's themes to singing Nuttall's songs.

Juvenile Nuttall's Sparrows in the laboratory begin singing (the practice stage) nine months after hatching (Konishi 1965, Baptista and Petrinovich 1986, Nelson et al. 1995); however, fledgling Nuttall's Sparrows in the wild may sing subcrystallized song by 28 days of age (Baptista et al. 1993b). Song may crystallize by 90 days when juveniles first establish territories. Matched countersinging and repertoire reduction has been observed in January (DeWolfe et al. 1989). Our observations of G1 indicate, however, that whittling of repertoire size is not confined to the early part of the year but may take place as late as August or in whatever period a bird singing several songs finally settles on a territory.

Playback studies have shown that Nuttall's Sparrows respond strongly to local dialects

but hardly at all to song of the alien subspecies *pugetensis* (Petrinovich and Patterson 1981). In contrast, G2's three Nuttall neighbors responded strongly to playback of his alien Gambel's song. By associative learning, these neighbors had learned to react to his alien dialect (see Richards 1979).

To our surprise, five out of seven White-crowns holding territories out of earshot from G2 also responded to playback of his Gambel song (Cebrian, unpubl. data). These individuals held territories 0.31 to 2.1 km from G2's territory (median 2.07 km). This indicates that these aggressive individuals must have interacted with wintering Gambel's Sparrows or with G2 himself. Since wintering Gambel's Sparrows are sometimes territorial (see above), storing their songs enables Nuttall's Sparrows to identify potential competitors. Storage of alien songs by White-crowns, namely those of Song Sparrows (*Melospiza melodia*), to be used for recognition of competitors, has been documented previously (Baptista 1990, Catchpole and Baptista 1988).

It is thus likely that more Nuttall's Sparrows acquire songs of Gambel's Sparrows in the wild than are detected. However, due to matched countersinging with neighbors during settling, local dialects are selected for and rare alien dialects fall into disuse. Elimination of song from a bivalent repertoire in a White-crown's second year has been documented previously (Baptista and Morton 1988). If G1 behaved likewise, then our playback experiments indicate that such lost songs may be recalled and vocalized with stimulation by intense playback even a year later.

In summary, if there are barriers to Nuttall's Sparrows learning songs of Gambel's Sparrows in the wild, it is clear that they are not insurmountable. Under appropriate conditions, Nuttall's Sparrows can indeed learn songs of the other subspecies. Incidence of Nuttall's Sparrows learning Gambel's songs may be rare only because the latter are rare as winter visitants. Local dialects are preserved by matched countersinging and narrowing of song repertoires, and the narrowing process may take place well beyond the start of the breeding season. Moreover, a previously used song absent from the current repertoire may be evoked by matched countersinging.

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LUIS F. BAPTISTA, ANDREA JESSE, DOUGLAS A. BELL, AND CHRISTIAN CEBRIAN, *Dept. of Ornithology and Mammalogy, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.* *Received 25 Sept. 1996, accepted 1 April 1997.*

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Status of Neotropical migrants in three forest fragments in Illinois.—Species that breed in temperate North America but migrate to the tropics in the nonbreeding season (hereafter "Neotropical migrants") have become a focal point of ornithological research and management (e.g., Hagan and Johnston 1992, Martin and Finch 1995). This concern and interest results from the finding that some Neotropical migrants have shown clear and unambiguous declines throughout their ranges (e.g., Cerulean Warbler [*Dendroica cerulea*], Robbins et al. 1992), and most species have shown pronounced declines in isolated woodlots (Askins et al. 1990) and/or some geographic regions (James et al. 1996). Regardless of how widespread declines are, high levels of nest parasitism by cowbirds and increased levels of nest predation on these species are phenomena worthy of research and management concern.

Reproductive success of many Neotropical migrants varies dramatically across their ranges in response to the degree of forest fragmentation (Robinson et al. 1995). Generally, the greater the fragmentation and the lower the proportion of forest in the landscape, the lower the reproductive success (Robinson et al. 1995). This pattern suggests that source-sink models of population structure may be very applicable to forest-nesting neotropical migrants (Brawn and Robinson 1996). The contiguous "cornbelt" region of Illinois, Indiana, Ohio, Missouri, and adjacent states may represent one of the largest reproductive sinks for these species (Brawn and Robinson 1996). We tested the generality of this idea by using mist nets to monitor reproductive success in three woodlots in east-central Illinois, including two of the largest forest fragments in this region.

Study area and methods.—We selected three forest fragments that appeared to be the best available habitat in east-central Illinois for area-sensitive, forest-nesting neotropical migrants. Two sites, Fox Ridge State Park (454 ha) in Coles County and Walnut Point State Park (223 ha) in Douglas County, were the largest contiguous blocks of forest in their respective counties. The third site, Baber Woods, is a Nature Conservancy preserve that, although much smaller (20 ha), is one of the largest stands of virgin timber in east-central Illinois. Vegetation was sampled at each site, using 12 0.04 ha circular plots (James and Shugart 1970), located randomly along the mist-net line.

We mist netted birds in each woodlot following the methods of Robinson (1992; see also Bollinger and Linder 1994). Twenty nets (black, 36 mm mesh, 12 m) were strung end-to-end along the net line and opened for three consecutive days from 06:00–12:00 CDT. Two, 20-net lines were sampled at Fox Ridge and Walnut Point but only one line at Baber Woods because of its smaller size. Each line was sampled twice, once between 20 June and 6 July 1993 and once between 7 July and 23 July 1993. Lines were located in the centers of each

TABLE 1

CHARACTERISTICS OF THREE FOREST FRAGMENTS IN CENTRAL ILLINOIS

	Baber Woods	Fox Ridge State Park	Walnut Point State Park
	General		
Total size (ha)	20	454	223
Forest interior (ha)[a]	0	31	9
Slope (°)[b]	2	24	6
	Vegetative[b]		
Tree density (stems/ha)[c]	586	529	598
Total basal area (m^2/ha)	45	30	42
White oak dominance (% of basal area)	29	29	45
Hickory dominance (% of basal area)	14	33	13
Sugar Maple dominance (% of basal area)	21	16	9
Shrub density (stems/ha)[d]	1802	3489	2917
Most common shrub	Sugar maple	Sugar maple	Sugar maple
Canopy coverage (%)	91	84	89
	Landscape		
Percent of land ≤10 km from center of site in forest	17	33	13
Percent of land ≤10 km from site in forest interior	<1	3	<1

[a] Forest interior is forest ≥250 m from edge of forest fragment.
[b] Mean of 12 random locations.
[c] Trees are woody stems ≥7.6 cm diameter at breast height (DBH).
[d] Shrubs are woody stems <7.6 cm DBH but at least 1.4 m high.

forest fragment (≥200 m from any edge at Fox Ridge and Walnut Point and ≥50 m from any edge at Baber Woods).

All birds that were captured were banded with U.S. Fish & Wildlife Service bands, aged by plumage characteristics and skull pneumatization (Pyle et al. 1987, USFWS 1991), measured, and released. Birds were aged as either adult, "after-hatching-year" (AHY), or recently fledged, "hatching-year" (HY) birds.

We analyzed our mist-netting data primarily through chi-square tests of the numbers of birds captured. Tests have one degree of freedom unless noted otherwise. We have followed the categorizations of Whitcomb et al. (1981) and Freemark and Collins (1992) to distinguish Neotropical migrants from permanent residents and short-distance migrants. These references were also used to categorize species as "forest interior," "interior/edge," or "edge" species. Permanent residents and short-distance migrants are referred to collectively as "local" species (Bollinger and Linder 1994). Finally, we determined the amount of forest and amount of forest interior (forest ≥250 m from an edge) within a 10-km radius of the center of each study site (as in Robinson et al. 1995) using 150 random locations on topographic maps.

TABLE 2

NUMBERS OF BIRDS MOST COMMONLY CAPTURED IN MIST NETS FROM LATE JUNE THROUGH MID-JULY IN THREE FOREST FRAGMENTS IN CENTRAL ILLINOIS ALONG WITH RATIOS OF HATCHING YEAR (HY) BIRDS TO ADULTS (AHY)

Species	Baber Woods	Fox Ridge	Walnut Point	Overall HY/AHY
	Neotropical migrants[a]			
Wood Thrush (*Hylociclila mustelina*)	29	3	5	0.09
Acadian Flycatcher (*Empidonax virescens*)	3	10	2	0.15
Scarlet Tanager (*Piranga olivacea*)	2	3	4	0.00
Red-eyed Vireo (*Vireo olivaceus*)	2	6	0	0.00
Eastern Wood-Pewee (*Contopus virens*)	0	5	2	0.00
Louisiana Waterthrush (*Seiurus motacilla*)	0	5	0	0.25
All Neotropical Species	41	40	17	0.09
	Local[b]			
Downy Woodpecker (*Picoides pubescens*)	2	8	15	2.57
Northern Cardinal (*Cardinalis cardinalis*)	2	6	4	0.33
Blue Jay (*Cyanocitta cristata*)	0	2	6	0.00
Brown-headed Cowbird (*Molothrus ater*)	5	1	1	0.75
Tufted Titmouse (*Parus bicolor*)	6	0	0	1.00
Hairy Woodpecker (*Picoides villosus*)	1	1	3	0.67
All Local Species	23	24	31	0.63

[a] Other neotropical migrants captured included (in decreasing order of abundance)—Ovenbird (*Seiurus aurocapillus*), Indigo Bunting (*Passerina cyanea*), Worm-eating Warbler (*Helmintheros vermivorus*), Kentucky Warbler (*Oporornis formosus*), Ruby-throated Hummingbird (*Archilochus colubris*), Great Crested Flycatcher (*Myiarchus crinitus*), Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat (*Icteria virens*), and White-eyed Vireo (*Vireo griseus*).

[b] Local species included both permanent residents and short-distance migrants. Other species captured included (in decreasing order of abundance)—Carolina Wren (*Thryothorus ludovicianus*), American Robin (*Turdus migratorius*), White-breasted Nuthatch (*Sitta carolinensis*), Red-bellied Woodpecker (*Melanerpes carolinus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Sharp-shinned Hawk (*Accipiter striatus*).

Results.—All three sites were fairly similar vegetatively. White oak (*Quercus alba*) had the highest basal area in each site, and sugar maple (*Acer saccharum*) and hickories (*Carya* spp.) were also abundant. However, Baber Woods and Walnut Point were flatter than Fox Ridge, and Baber Woods had larger trees, on average, than the other two sites. All three sites were found in landscapes with little forest cover and almost no "forest interior" (Table 1).

A total of 176 birds were captured at all three sites combined (Table 2). Of the 138 adults (AHY birds), 65% were Neotropical migrants (62% were "interior" or "interior/edge" species). Only 8% of all Neotropical migrants (all species combined) were HY birds, compared with 38% for local species ($\chi^2 = 23.6$, $P < 0.001$). The percentage of Neotropical migrants that were HY birds did not vary among the three sites ($\chi^2 = 0.36$, df = 2, $P > 0.75$). However, with all species combined (neotropical + local), the percentage of birds that were HY did vary markedly by nest type with cavity-nesting species having 51% HY birds, 15% for ground nesting species, and 8% for all others ($\chi^2 = 34.8$, df = 2, $P < 0.001$). Among the adult Neotropical migrants that we captured, 59% were males compared with 44% for local species ($\chi^2 = 2.9$, $P < 0.10$). Finally, based on 10 nests of neotropical migrants that we found on an ad hoc basis, daily predation rate averaged 6.2% (and 5% for four Wood Thrush nests), so that nest success over a 30 d nesting cycle would be 15% (Mayfield 1975). Three of these nests were parasitized by cowbirds.

Discussion.—Our data appear to support the conclusion of Robinson (1992) and Brawn and Robinson (1996) that much of the midwestern United States represents a population sink for forest-nesting neotropical migrants. However, using constant effort mistnetting (CEM) to estimate reproductive success is not without problems (Robinson 1992, Nur and Guepel 1993). The few attempts to validate CEM (e.g., Feu and McMeeking 1991, Nur and Geupel 1993) as a means of estimating reproductive success have shown that there is significant variation both within and among species in CEM's ability to track temporal changes in local productivity. Certainly more work is needed in validating CEM methodology, given its widespread use in large scale monitoring programs in North America (DeSante et al. 1993) and Britain (Baillie 1990).

Nevertheless, the extremely low percentage of HY Neotropical migrants that we captured (relative to local species) suggests that these species, as a group, are probably not able to offset adult mortality with local recruitment, even in the largest forest fragments in east-central Illinois. One explanation for low recruitment of Neotropical migrants in forest fragments is that populations are largely unmated males (e.g., Gibbs and Faaborg 1990). This was supported to some extent by our data (e.g., we captured only three male Ovenbirds); however, 44% of neotropical adults were females. More significant, in our opinion, are extremely high predation levels suggested by this study and others in Illinois (Robinson 1992, Bollinger and Peak 1995, Linder and Bollinger 1995, Brawn and Robinson 1996). Given that little can likely be done to reduce forest fragmentation in the agricultural Midwest, these results underscore the need to maintain heavily forested landscapes in nearby areas (e.g., Ozark mountains; Robinson et al. 1995, Brawn and Robinson 1996).

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ERIC K. BOLLINGER, BRIAN D. PEER, AND ROGER W. JANSEN. *Dept. Zoology, Eastern Illinois University, Charleston, Illinois 61920.* (Present address BDP: *Dept. Zoology, University of*

Manitoba, Winnipeg, Manitoba, R3T 2N2; present address RWJ: *105 S. Oak, Teutopolis, Illinois 62467*). *Received 15 Aug. 1996, accepted 10 Feb. 1997.*

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Diet and hunting behavior of the Plumbeous Kite.—The Plumbeous Kite (*Ictinia plumbea*) forms a superspecies or is conspecific with the Mississippi Kite (*I. mississippiensis*), (AOU 1983, Parker 1988). It inhabits humid lowlands from eastern Mexico south to Bolivia, Argentina, and Paraguay, while the Mississippi Kite breeds widely across the southern United States and winters in South America (Brown and Amadon 1968). The Plumbeous Kite is migratory at the southern and northern limits of its range. Although the diet and hunting behavior of the Mississippi Kite have been relatively well studied (Skinner 1962, Parker 1974, 1988, Evans 1981, Glinski and Ohmart 1983), information about the Plumbeous Kite has been based on observations at one nest in Ecuador by Skutch (1947) and a handful of casual observations (Haverschmidt 1962, Ferrari 1990). Here we present data collected over a four-year period on the diet and hunting behavior of Plumbeous Kites at a Central American lowland site.

Study site and methods.—We studied Plumbeous Kites in Tikal National Park, Petén, Guatemala, from 1991–1994 as part of The Peregrine Fund's "Maya Project." Tikal National Park covers 576 km^2 in NE Guatemala (17°13′N, 89°38′W). Elevation is 200–250 m amsl, topography gently rolling, and the climate tropical, with an annual rainfall of about 1350 mm. The rainy season begins from mid-May to late June, with highest rainfall in September, and a pronounced dry season occurs from February until May or June. The semideciduous tropical forest varies along a subtle topographic continuum. In well-drained sites it is 25–30 m tall with closed canopy, open understory, and diverse tree species, while in low-lying areas, it is lower (10–15 m) with more open canopy, dense understory, and partly different tree species composition. Forest vegetation, climate, and land-use patterns of the Tikal area were described by Schulze (1992) and Whitacre et al. (1993, 1995). Tikal National Park is covered mostly by unbroken primary forest, with some areas of light selective logging prior to 1969. Study nests were located near clearings around Maya ruins and park facilities.

Plumbeous Kites arrived at Tikal in late February, began nesting in March, fledged young in June and July, and departed in August (Vásquez et al. 1992; D. Whitacre, unpubl. data). Observations of prey deliveries were conducted at six nests—two each in 1991, 1992, and 1994. In 1991 and 1992, most nest observations were full day, while in 1994 most were from two to six hours. Prey deliveries were observed using a 30-power spotting scope and binoculars at a distance of 20–30 m. Prey items were delivered to nestlings in the manner described by Skutch (1947): they were carried to the tree either in the bill or feet but always transferred to the bill before landing in the nest tree, and retained there as the bird walked to the nest, allowing sufficient time for identification. In 1994, we studied hunting behavior concurrently with nest observations, focusing on adults at two nests. We watched whichever pair member was hunting at the time, and when it joined flocks of foraging kites, we still observed one individual throughout, though not necessarily the same individual observed previously. We described all hunts, identity and position of quarry, and outcome. For success calculations, a hunt was defined as a completed attempt to seize an individual quarry. Rarely did kites make multiple attempts to seize the same quarry, but when they did, these were regarded as separate hunts. For statistical analyses, we used multiple random permutation procedure (MRPP) Chi-square tests (Berry and Mielke 1986).

Results.—We observed delivery of 702 prey items, 655 of which we identified to some

level (Table 1). Because the bulk of the 47 unidentified prey items was likely insects, the diet is most accurately described as percent of identified prey rather than total prey. Considering the six nests individually, insects averaged 92.5% of prey (N = 6, SD = 8.1), lizards 6.0% (SD = 6.6), snakes 1.1% (SD = 2.0), birds 0.3% (SD = 0.7), bats 0.2% (SD = 0.5), and frogs 0.1% (SD = 0.2). Use of biomass estimates would slightly increase the importance of vertebrates but would not alter basic patterns.

Cicadas and beetles were the most commonly captured insects, although dragonflies, orthopterans, lepidopterans, and hymenopterans were also taken (Table 1). The relative importance of these orders varied between years. At 1991 and 1994 nests, cicadas and beetles dominated the diet, while in 1992, dragonflies, orthopterans, and lepidopterans figured more prominently. Especially striking was the large proportion of lizards at 1992 nests, where few cicadas were taken (Table 1). Overall, 34.4% of insect prey was unidentified; these may have included additional orders and may have systematically included smaller insects.

Lizards taken included both the arboreal/scansorial genus *Norops* (formerly *Anolis*) and *Sceloporus*. *Sceloporus* were frequently observed on limestone Maya temples near which the kites nested and were uncommon in the forest at large. *Norops,* in contrast, were abundant on vegetation throughout the forest. All lizards brought to nests were small, estimated at <15 g. Only two bats were observed as prey items, both probably <15 g. All three birds taken were Northern Rough-winged Swallows (*Stelgidopteryx serripennis*), which nested abundantly in the ruins; it is possible these were fledglings. We witnessed one pair of kites capture a Northern Rough-winged Swallow via a cooperative hunt (Seavy, pers. obs.). The few frogs and snakes brought to nests were small, with estimated weights <10 g.

Plumbeous Kites used two foraging techniques—aerial hunts (hunts launched from flight) and perch hunts (hunts launched from a perch). Aerial hunts were launched at flying prey from extensive prospecting flights during which the kites soared anywhere from canopy level to several hundred m above. In aerial hunts, insect prey were captured in one of three ways: (1) quick grabs—when birds did not perceptibly alter their flight path and reached out to seize nearby insects, (2) short, flapping climbs to seize an insect above, and (3) diving pursuits—when kites attacked an insect below them by dropping into a long dive or shallow swoop, seizing the insect as they pulled out at the bottom. These attacks were up to 100 m but usually 10–40 m in length. In hunts launched from a perch, the birds would either drop from the perch into a stoop or make a short, flapping flight to capture prey. Unlike the aerial hunts, perch hunts sometimes culminated with the kites making contact with the forest canopy or ground in pursuit of prey. Prey was always captured with the talons.

Two hundred forty-six hunts (61%, N = 403) were successful. Sixty-nine percent (276) were initiated from soaring flight and the rest from perches. Aerial hunts were directed at flying insects and were significantly more successful (65%; 179 of 276) than hunts from perches (53%; 67 of 127) (P = 0.002, MRPP Chi-square test). Of hunts launched from perches, 87% were directed at insects in flight, and 13% were directed at insects or small lizards in the forest canopy or on the ground. Perch hunts at flying insects were less successful (55%, 60 of 110) than aerial hunts (P = 0.06, MRPP Chi-square test) but similar to perch hunts for quarry in the canopy or on the ground (41.2% successful; 7 of 17) (P = 0.317, MRPP Chi-square test). Hunts for quarry in the forest canopy or on the ground made up only 4% of all observed hunts.

Hunting activity peaked strongly during mid-morning, was lowest during early afternoon, and increased gradually thereafter to a low peak near sunset (Fig. 1). Most hunts during the peak hunting hours of 07:00 to 11:00 CST were launched from soaring flight at flying insects, while perch hunting predominated in early morning and throughout the afternoon and evening (Fig. 1). On six occasions in 1994, groups of 5–14 Plumbeous Kites and 1–5 American Swallow-tailed Kites (*Elanoides forficatus*) were observed foraging together over

TABLE 1

FREQUENCY OF PREY ITEMS DELIVERED TO SIX PLUMBEOUS KITE NESTS AT FOUR TERRITORIES (A, B, C, AND D) IN TIKAL NATIONAL PARK, GUATEMALA: PERCENTAGES BASED ON IDENTIFIED PREY ITEMS

	1994a N (%)	1994b N (%)	1992b N (%)	1992c N (%)	1991c N (%)	1991d N (%)	Total N (%)
Homoptera	41 (24.55)	57 (35.20)	1 (1.22)	7 (6.31)	29 (39.19)	12 (20.34)	147 (22.44)
Coleoptera	37 (22.16)	53 (32.70)	0 (0.00)	0 (0.00)	6 (8.11)	20 (33.90)	116 (17.71)
Odonata	2 (1.20)	2 (1.23)	19 (23.17)	33 (29.73)	3 (4.05)	4 (6.78)	63 (9.62)
Orthoptera	2 (1.20)	3 (1.85)	8 (9.76)	16 (14.41)	4 (5.41)	2 (3.39)	35 (5.34)
Lepidoptera	2 (1.20)	0 (0.00)	8 (9.76)	8 (7.21)	2 (2.70)	1 (1.69)	21 (3.21)
Hymenoptera	6 (3.59)	0 (0.00)	1 (1.22)	2 (1.80)	8 (10.81)	1 (1.69)	18 (2.75)
Unident. insects	70 (41.90)	44 (27.16)	27 (32.93)	31 (27.93)	21 (28.38)	17 (28.81)	210 (32.06)
Total insects	160 (95.80)	159 (98.15)	64 (78.05)	97 (87.39)	73 (98.65)	57 (96.61)	610 (93.13)
Lizards	2 (1.20)	2 (1.23)	14 (17.07)	12 (10.81)	1 (1.35)	2 (3.39)	33 (5.04)
Snakes	0 (0.00)	0 (0.00)	4 (4.88)	2 (1.80)	0 (0.00)	0 (0.00)	6 (0.92)
Frogs	0 (0.00)	1 (0.62)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.15)
Birds	3 (1.80)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	3 (0.46)
Bats	2 (1.20)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.30)
Total verts.	7 (4.20)	3 (1.85)	18 (21.95)	14 (12.61)	1 (1.35)	2 (3.39)	45 (6.87)
Unident. prey	2	8	5	19	10	3	47
Total ident. prey	167	162	82	111	74	59	655
Total prey	169	170	87	130	84	62	702

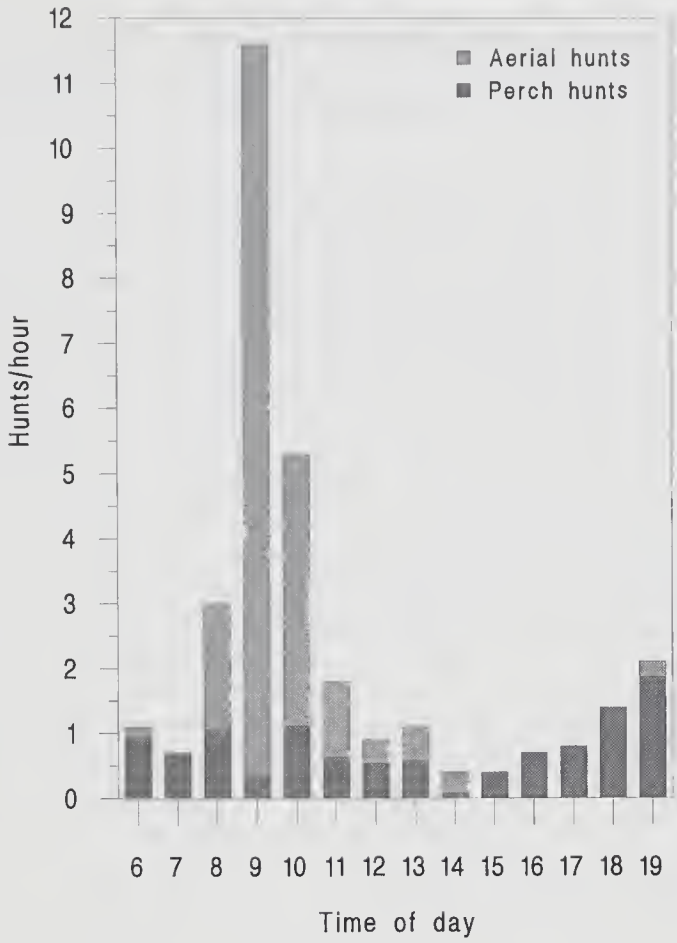

FIG. 1. Diel pattern of Plumbeous Kite hunts launched from flight and from perches at two nests at Tikal, Guatemala (nests 1994a and b, combined data).

the forest. These group foraging bouts were observed between 07:50 and 09:10, and lasted from 5–60 min. This foraging took place 50–200 m above the canopy as the kites repeatedly grabbed at small insects with their feet and fed on the wing.

Discussion.—The diet and hunting behavior of Plumbeous Kites were similar to those of the Mississippi Kite (Glinski and Ohmart 1983, Parker 1988). In both species, insects comprised the bulk of the diet, with small vertebrates providing the remainder. Cicadas were the predominant prey in both Arizona and Tikal, and Glinski (pers. comm.) emphasized those authors' conviction that cicadas are central to the Mississippi Kite's ecology in Arizona. In Brazil, Plumbeous Kites preyed on cicadas flushed from vegetation by small primates (Ferrari 1990).

Diel patterns of perch and aerial hunting, similar to those we observed in Tikal, have been noted in Mississippi Kites (Glinski and Ohmart 1983). Scarcity of atmospheric lift and insect flight activity may explain the predominance of perch hunting during the cool, early morning, but these explanations do no apply to the hot afternoon hours. Aerial hunts at dawn and dusk may have been directed at insect mating swarms, especially of ants and termites, which often occur at such hours (Whitacre 1992).

Annual variation in the composition of the nestling diet may suggest a functional complementarity between certain large insects and small vertebrates in the diet of this raptor. It is our impression that, at Tikal, populations of some large insects, including cicadas and

some beetles, are generally more labile than those of small reptiles. We speculate that fluctuations of insect populations may largely dictate the degree of predation pressure at a given point in time directed at small vertebrate prey by Plumbeous Kites and other raptors with mixed insect/vertebrate diets.

Though much Plumbeous Kite hunting occurred within 200 m of the nest, much also occurred farther afield. The extent to which the prey base of Plumbeous Kites may be economically defensible is open to question. Areas of forest yielding cicadas, beetles, and lizards may be defensible, but ephemeral aggregations of dragonflies and other flying insects probably are not. It is unknown whether aggregations of foraging individuals resulted simply from gregariousness, from independent discovery of local prey concentrations, or by kites cueing in on the foraging motions of other individuals ("network foraging" or "local enhancement"; Thorpe 1956, Pulliam and Millikan 1982), a behavior that could aid these highly mobile birds to exploit rich but ephemeral food sources such as insect swarms.

Arthropod abundance at Central American lowland sites typically reaches a strong annual peak soon after the onset of the rainy season, often dropping to lower, dry season levels during the latter half of the rainy season (Janzen 1973, 1980, Levings and Windsor 1982). Weekly insect sampling begun in December 1994 at Tikal showed the same pattern, with insect numbers increasing during the first weeks of the rainy season and declining thereafter (D. Whitacre, unpubl. data). Plumbeous Kites at Tikal fledged during the first few weeks of the rainy season. Such reproductive timing, with the high food demands of nestling young and the fledging event both taking place at a time of maximal insect abundance, conforms to the pattern prevalent among insectivorous birds in Central America (Skutch 1950). Likewise, the high hunting success rates and diet of mainly insects and lower vertebrates, in combination with the very small degree of sexual size dimorphism of the Plumbeous Kite (Bierregaard 1978), conform well with patterns established to date among these factors within the Falconiformes (Temeles 1985).

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NATHANIEL E. SEAVY, *17142 Lemolo Shr. Dr. N. E., Poulsbo, Washington 98370*; MARK D. SCHULZE, *Dept. of Biology, Pennsylvania State Univ., University Park, Pennsylvania 16802*;

DAVID F. WHITACRE, *The Peregrine Fund, 566 W. Flying Hawk Lane, Boise, Idaho 83709*; AND MIGUEL A. VÁSQUEZ, *Parque Nacional Tikal, Petén, Guatemala.* *Received 27 Feb. 1996, accepted 27 Feb. 1997.*

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European Starlings nesting in southern Baja California, Mexico.—The European Starling (*Sturnus vulgaris*) has become abundant across North America since its introduction in New York in 1890. Starlings have been recorded breeding in Baja California as far south as Cataviña (Fig. 1) (Wilbur 1987) and now occupy virtually all the suitable habitat in the northern portion of the peninsula (Short and Crossin 1967). Some incidental winter records have also been reported in southern Baja California (Wilbur 1987, Howell and Webb 1992). Until recently, Southern Baja may be one of the least disturbed areas in the world. The desert is dry and hot (average annual precipitation, 150.6 mm; mean annual temperature, 22.1°C to 23.4°C, maximum 44°C) with a dense sarcocaulescent scrub vegetation dominated by cardon cactus (*Pachycereus pringlei*), dagger cactus (*Stenocereus gummosus*), mesquite (*Prosopis articulata*), palo verde (*Cercidium microphyllum*), Adam's tree (*Fouquieria diguetii*), plum tree (*Cyrtocarpa edulis*), copal (*Bursera* spp.), lomboy (*Jatropha cinerea*), and cholla (*Opuntia cholla*) (Wiggins 1980). Cardons are giant columnar cacti with a principal trunk and generally 4–12 branches starting 3–4 m from the ground. Almost every 6–8 m cardon contains a cavity in one of the branches, cavities that generally were excavated by woodpeckers. These holes are extensively used by both primary and secondary cavity-nesting birds (Rodríguez-Estrella, unpubl. data).

Human activity in the desert of Baja California was still minimal a decade ago. In the 1950s, the Federal government strongly promoted human colonization and increased agricultural activity in the nearly uninhabitated peninsula of Baja California. Subsequently, agriculture and livestock activities have increased along the peninsula. Agriculture was only progressing slowly until the end of the 1980s (Gobierno del Estado 1992). An increase in areas dedicated to agriculture has been recently detected (RR-E pers. obs.). The increase has been concentrated mainly in the Ciudad Insurgentes-Ciudad Constitución, Centenario-Chametla, Los Planes, Santiago-La Ribera, and El Carrizal regions (Fig. 1). These changes may have benefited starlings for colonization.

In this paper, we report the first nesting records of the European Starling in the Cape region, the southernmost record in Baja California, and discuss potential effects nesting starlings might have on the native cavity-nesting bird species in the area.

From May through July 1995, while doing breeding bird censuses in Baja California Sur, we found a European Starling nest with nestlings and observed several other instances of starling breeding activity. We recorded starlings in 16% of the 117 two-hour observational points from Loreto to Cabo San Lucas (Fig. 1). Records were significantly more frequent in human-transformed areas with field crops and rural settlements (14 of 39 points) than in remote areas with natural vegetation (5 of 78 points) ($\chi^2 = 13.9$; 1 df; $P < 0.001$). The mean number of starlings counted was 2.6 ± 2.6 (range 1–10; N = 19 observations). Record sites are shown in Fig. 1.

The starling nest was found on 26 May at the edge of a field crop in a cultivated area containing some scattered trees (Fig. 1). Grazing pastures and corn fields were located within 100 m of the nest area, and some relictual patches of natural vegetation, including cardon and dagger cactus, mesquite, palo verde, Adam's tree, lomboy, and cholla bordered the area. The nest was in an old woodpecker hole in a 4.7 m cardon cactus. The nest cavity was 4.2

FIG. 1. Localities where starlings have been recorded in southern Baja California (Mexico). The square represents the previous southernmost breeding record. The star indicates our finding of one nest. Solid circles are localities where starlings were observed. Open circles are other localities mentioned in text.

m above the ground, and the cavity entrance was oriented in a NNW direction. Two apparently healthy nestlings, almost fully feathered (ca 15 days old), were in the cavity.

Two other possible nests were found in cardon cavities on 29 May in Los Planes and 1 June in Ciudad Constitución (Fig. 1). Although we did not climb to these cavities, breeding was likely because adults had the yellow-orange color in the bill (see Howell and Webb 1995) and entered both holes. A third adult bird was observed several times carrying food towards a cardon patch in Ciudad Insurgentes. These records clearly show that the European Starling has continued to expand its breeding range into southern Baja California. It has moved more than 800 km to the south of the last breeding record (Howell and Webb 1992). Previous studies (1989 to 1994) had not detected starlings during the breeding season or

nesting birds in southern Baja (Howell and Webb 1992; Rodríguez-Estrella et al., unpubl. data; J. Guzmán, pers. comm.).

The increased incidence of starlings in southern Baja California may be correlated with an increase in agricultural and cattle-raising activities during the last decade in this area (see Gobierno del Estado 1992). That their distribution is significantly associated with human-transformed areas suggests the increase in these practices in the region may have promoted a range expansion of the European Starling in Baja California as has recently happened with other bird species, including the White-tailed Kite (*Elanus leucurus*), Brown-headed Cowbird (*Molothrus ater*) and Western Meadowlark (*Sturnella neglecta*) (see Howell and Webb 1992, Rodríguez-Estrella et al. 1995).

The European Starling has been considered to be the cause of declines of some bird species in North America because of competition for nest sites (Weitzel 1988, Kerpez and Smith 1990, Ingold 1994). Interference competition imposed by starlings on native cavity-nesting species seems to be more intense in habitats where nest sites are limited (Weitzel 1988) and where an overlap in nesting phenologies exists (Ingold 1994). In Baja California, there are eight cavity-nesting bird species, all of which can nest in cardon holes. These include American Kestrel (*Falco sparyerius*), Gila Woodpecker (*Melanerpes uropygialis*), Northern Flicker (*Colaptes auratus*), Ladder-backed Woodpecker (*Picoides scalaris*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Cactus Wren (*Campylorhynchus brunneicapillus*), House Finch (*Carpodacus mexicanus*), and Violet-green Swallow (*Tachycineta thalassina*). At present, all of these species are common in areas both with and without starlings. Although nest sites are not likely to be limited (density of cardons with holes is high), the nesting phenology of starlings overlaps that of most native cavity-nesting birds. Thus, all these bird species could be adversely affected in the future by starling competition as several studies in other areas have shown (especially for woodpeckers and flycatchers; Weitzel 1988, Kerpez and Smith 1990, Ingold 1994, Rendell and Robertson 1994).

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RICARDO RODRÍGUEZ-ESTRELLA,[1,2] JAVIER BUSTAMANTE,[2] AND M. CARMEN BLÁZQUEZ,[1,2] [1]*Centro de Investigaciones Biológicas del Noroeste, Div. Biol. Terr., Apdo. Postal 128, La Paz 23000 B.C.S., México.* [2]*Estación Biológica de Doñana, Avda. María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain.* *Received 22 June 1966, accepted 15 Feb. 1997.*

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Stomach flushing: sampling the diet of Red-cockaded Woodpeckers.—Stomach flushing is one of several non-destructive methods recommended by Rosenberg and Cooper (1990) to ascertain diets of wild birds. Brensing (1977) and Jenni et al. (1990) described the method and documented its lack of effects on the short term survival of passerines. Moody (1970) reported some mortality during use of the procedure on nestlings. He did not study the effects of the procedure on subsequent survival. Here I describe a similar technique I used on adult Red-cockaded Woodpeckers (*Picoides borealis*) in the Apalachicola National Forest in northern Florida. I also describe tests of whether flushing affected the fledging rates and survival of nestlings.

Methods.—To flush the stomach and esophagus of a Red-cockaded Woodpecker, I used a plastic tube of 4 mm outside diameter attached to a 12 cc syringe filled with sterile 0.9% solution of sodium chloride. The tube was moistened with the saline solution for lubrication and inserted into the bird approximately 9 cm. No force was required. Special care must be taken to align the tube properly at the point where the esophagus enters the body cavity to insure easy insertion. Once the tube entered the stomach it slid to the bottom, stopping just above the entrance to the gizzard. The bird was then inverted over a plastic cup so that, as fluid was forced into its stomach, the excess fluid plus the stomach contents flowed into the cup. The process was completed in less than two minutes.

Thirty adult woodpeckers were flushed between August 1993 and May 1994. An additional 21 adult birds were flushed between June 1994 and December 1994. Approximately four birds were flushed per month. Each bird was captured as it went to roost for the night. To avoid stress-related mortality, flushing was not attempted on nights when the dry-bulb temperature was expected to fall below 4°C. Although no birds appeared to be harmed by the process, the first ten were checked for evidence of weakness or mortality in the first days after they were flushed. In each case the flushed bird was still present one week later. Because adult Red-cockaded Woodpeckers are highly territorial and often remain in the same territory for their adult lives, mortality rates of flushed and non-flushed individuals could be estimated by subsequent monitoring. Direct calculation of adult mortality rates is difficult because some movement among sites occurs. The criterion I used was a comparison of the rates at which flushed and non-flushed birds disappeared from their social groups, as measured by an annual census of banded birds. This census was conducted at the end of the nesting season in a sample population of 160 of the approximately 500 social groups on the Apalachicola Ranger District of the Apalachicola National Forest.

The same technique used to flush adults was used on nestlings. They were pulled from their nests with a noose at 5–8 days of age (Jackson, 1982). Each nestling was banded and weighed prior to being flushed. Only the largest nestling in each nest was flushed. In the non-flushed control group, nestlings were pulled, weighed and banded but not flushed. In 1993, 21 nestlings were flushed; in 1994 an additional 22 nestlings were flushed.

Mortality rates of nestlings were determined by visiting each social group 30 days after hatching and observing each group until all birds had been identified by their unique color bands. If color bands were not seen on the first visit, additional visits were made until all birds had been identified. One juvenile bird had to be eliminated from the analysis for 1994 because only one of the two nestmates fledged. That juvenile's color bands were not seen prior to its disappearance. In the analysis of nestling mortality rates, data for each year were analyzed separately and jointly.

Results.—Adult Red-cockaded Woodpeckers were not affected by the flushing process. Surprisingly, flushed birds showed even higher retention rates (83%) than did non-flushed birds (71%) (Table 1), but these differences were not significant ($\chi^2 = 2.0$, $P = 0.16$ N = 30, 161). In the 1994–1995 season, 81% of the flushed adult birds remained in their groups through the 1995 nesting season compared to 73% for the non-flushed birds ($\chi^2 = .62$, $P = 0.43$ N = 21, 211). Although there were differences in the retention rates of males and females, these differences were ignored in the analysis, because in most cases flushed birds had higher retention rates than did non-flushed birds.

Stomach flushing of the largest nestling in each nest had no apparent immediate effects, and all flushed nestlings were returned to their nests. Of the 21 birds flushed in June 1993, 10 (47%) fledged. This percentage was lower than the fledging rate for all 264 nestlings banded in 1993 (72%) and lower than the fledging rate of other largest nestlings banded in June (58%). However the latter difference was not significantly different ($\chi^2 = 0.47$, $P = 0.40$, N = 21 flushed, 17 nonflushed).

Twenty-one additional nestlings that were the largest in their nest were flushed in 1994 and were compared to the 110 largest non-flushed nestlings banded in that year. Again the fledging rate of non-flushed birds (81%) was higher than that of flushed birds (62%). However, when other factors were examined, it became apparent that flushing was not the major cause of this result. Rates of fledging success declined as the season progressed. Eighty-four percent of the 96 non-flushed nestlings that hatched prior to 15 May in 1994 fledged, but only 57% of the 14 non-flushed nestlings hatched after 15 May fledged. Because in 1994 13% of the non-flushed, but 47% of the flushed nestlings were hatched after 15 May, this seasonal effect must be controlled in an evaluation of the effect of flushing. If only those nestlings that hatched early in the season are compared, the differences of 84% fledged for the non-flushed and 73% for the flushed, are not significant ($\chi^2 = 0.96$, $P = 0.32$, N = 96, 11). The same nonsignificant relationship holds true for late nestlings, of which 57% of the unflushed birds fledged, and 50% of the flushed birds fledged ($\chi^2 = 0.12$, $P = 0.73$, N = 14, 10).

When multiple 2 × 2 tables give similar results that are not significant, it is possible to combine their evidence and strengthen the analysis with a Mantel-Hansen test of common odds ratios (Snedecor and Cochran 1980). This test on the three chi square tests reported above gave a similarly nonsignificant result (single-tailed test, $P = 0.126$).

To test possible effects on nestmates of siblings that were flushed, data from late nests (in which eggs hatched after 15 May) in both years were combined into one analysis. Fledging rates of the second largest nestlings in nests in which the largest was either flushed or not flushed were compared. In late nests of 19 second nestlings with older sibs that had been flushed, only 26% fledged. Of the 22 second nestlings with older sibs that had not been flushed, 59% fledged. This difference is significant ($\chi^2 = 4.45$ $P = .035$ N = 41).

TABLE 1

RETENTION RATES BETWEEN ANNUAL CENSUSES TAKEN AT THE END OF THE BREEDING SEASON OF FLUSHED AND NON-FLUSHED ADULT RED-COCKADED WOODPECKERS

Category	Males		Females		Total			
	N	%	N	%	N	%	χ^2	*P*
Retained in 1994								
Flushed 1993	18	83%	12	83%	30	83%		
Non-flushed 1993	107	72%	54	65%	161	71%	2.0	0.157
Retained in 1995								
Flushed 1994	17	76%	4	100%	21	81%		
Non-flushed 1994	138	78%	73	63%	211	73%	0.62	0.43
Retained in 1995								
Flushed 1993[a]	15	100%	10	60%	25	84%		
Non-flushed 1993[a]	79	75%	35	71%	114	74%	1.18	0.28

[a] 1995 Retention of birds that were present in 1993 and 1994.

However, this effect was not seen in the sibs of flushed and non-flushed nestlings in early nests. In early nests 83% of 81 nestlings with older non-flushed sibs fledged, and 82% of 11 nestlings with flushed sibs fledged.

Discussion.—Direct studies of the diets of wild birds, although often relevant to research questions, are uncommon in the literature (see review by Rosenberg and Cooper 1990). This lack of diet work may be attributable in part to a desire not to damage the studied population. In the present study, stomach flushing had no statistically significant effects on subsequent survival of adult Red-cockaded Woodpeckers. In fact, there was higher (nonsignificant) survival of flushed adult birds which could not be due to the flushing procedure and is probably a random effect. This lack of an effect of flushing on adult survival supports the conclusions of Brensing (1977), who had flushed 2100 passerines and reported no loss in weight of recaptured birds. Ford et al. (1982), who used the technique on Australian passerines, reported virtually no mortality during the procedure, Jenni et al. (1990) flushed warblers and reported mortality of less than 1% during handling. These researchers were using short-term recapture rates of adult birds in mist nets to make assessments about survival rates. Their recapture rates were approximately 30% for both flushed and non-flushed birds. In my study, longer term differences could be assessed. Even so, the results still suggest that the procedure does not adversely affect the survival rates of adult birds.

Because the flushed nestlings and their brood mates did show a lower survival rate than the control groups, I recommend caution when considering the flushing technique for nestlings. The largest effect of the procedure was not on the flushed nestlings themselves but on their nestmates, where flushing of late season nestlings was associated with a significantly reduced survival rate of their sibs. Apparently some factor in the environment reduces the success rate of late nests and flushing causes additional stress. This environmental factor may be related to food abundance.

My observations indicate that woodpeckers often hatch more chicks than survive to banding age and that the mortality of these nestlings is related to competition among them for food. Siblings pulled from a nest at 5–8 days of age can have up to a 12 g difference in their weights between the largest and smallest nestling, even though hatching occurs almost simultaneously for the first two nestlings. The smaller nestlings usually appear emaciated and do not have the enlarged stomachs characteristic of healthy nestlings. This difference in fledging rate is most pronounced for the smallest nestlings in a nest. In both 1994 and 1995, the fledging rate of the third largest nestling at banding time was 12% less than that of the largest nestling. At the time of banding in 1994, even though sibs hatched at approximately the same time, there was a 2.1 g difference in the mean weights of the largest and the second largest nestling. This difference was associated with a 4% decrease in their survival. In 1995 there was a 2.5 g difference and a 5.5% difference in survival. Thus it appears that survival to fledging is highly sensitive to food resources. Perhaps the one time removal of stomach contents from the largest chick increased its subsequent demand for food and led to the reduced chances for survival of its nestmates, even though there was no apparent direct effect of the procedure on the survival of the flushed nestling.

I conclude that stomach flushing can be an effective non-destructive method of sampling the diet of small adult and nestling birds, including endangered species. Even so, only well-trained researchers should use it, and it is not recommended for use on nestlings in small populations. The full effect of the procedure on nestlings and their sibs is still unclear. Additional studies are needed on other species using larger sample sizes. Analyses of the samples collected in this study will be reported elsewhere (Hess and James, in press; James et al. 1997).

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CHARLES A. HESS, *Dept. of Biological Science, Florida State Univ., Tallahassee, Florida. 32306.* *Received 30 Oct. 1995, accepted 1 Feb. 1997.*

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Morphological differences among populations of House Sparrows from different altitudes in Saudi Arabia.—The House Sparrow (*Passer domesticus*) is widely distributed throughout the world, both as a result of introduction and natural spread from Africa (Summers-Smith 1988, 1990). Johnston and Selander (1973) examined geographical variation in House Sparrow populations from both North America and Europe and found that the degree of geographical variation within North America is less than in Europe. This is presumably because sparrows have relatively recently become established in North America. In this paper we study differences between two populations of House Sparrows (*P. d. indicus*) separated by only 150 km, and which are close to the center of their ancient range (Summers-Smith 1988).

Study area and methods.—We examined morphology of sparrows at two different locations in Saudi Arabia. The first is at Taif (21°04′N, 40°16′E, elevation 1900 m) and the second at King Abdul-Aziz University campus in Jeddah (21°30′N, 39°12′E) on the Red

TABLE 1

MEAN ± ONE SE FOR SEVEN MORPHOLOGICAL CHARACTERS FOR *PASSER DOMESTICUS INDICUS* IN SAUDI ARABIA[a]

	Males		Females	
	Jeddah (16)	Taif (34)	Jeddah (18)	Taif (26)
Mass	18.00 ± 0.39	23.54 ± 0.59	18.25 ± 0.25	19.46 ± 0.61
Wing length	73.13 ± 0.52	74.71 ± 0.46	71.22 ± 0.38	71.96 ± 0.39
Tail length	58.72 ± 0.79	55.09 ± 0.73	56.06 ± 0.59	52.65 ± 1.04
Tarsus length	18.78 ± 0.28	18.59 ± 0.22	18.81 ± 0.19	17.79 ± 0.38
Bill length	9.50 ± 0.12	9.81 ± 0.07	9.44 ± 0.12	9.69 ± 0.13
Bill depth	6.63 ± 0.20	6.28 ± 0.16	6.67 ± 0.10	5.60 ± 0.20
Bill width	6.06 ± 0.13	5.37 ± 0.09	6.11 ± 0.14	5.14 ± 0.09

[a] Mass in g; all other measurements are in mm. All values are means ± SE. Sample sizes are in parentheses.

Sea coast. The two locations, beside being separated altitudinally, are about 150 km apart. The habitat of the upland site in Taif is mainly a rural area, mostly arable farmland, whereas Jeddah is mainly suburban. Taif has a moderate climate, varying from 30°C in summer to 10°C in winter. Rain falls mostly in winter and late spring (ca 30 cm per year). Jeddah is about 10°C hotter, and rain falls mostly in winter (ca 5 cm per year).

We captured birds in mist nets at these sites throughout the years 1993–1995. Most trapping effort (76%) was in the month of November (out of the breeding season). We measured mass, wing length, tail length, tarsus length, beak length (distance from the foremost feathers of the forehead to the tip of the upper mandible), beak depth, and beak width (both at the base of the bill). We analyzed both geographical and sex differences.

To compare our results with those of other studies, we used results on published studies of the same subspecies (Gavrilov 1965, Gavrilov and Korelov 1968, Summers-Smith 1988, Saini et al. 1989). We also used unpublished data on this subspecies collected by T. D. Price in the Eastern Ghats of India (17°40′N, 82°30′E, elevation ca 850 m). In this study, sparrows were captured in the village of Lammasinghi, as part of a study investigating competition between the House and Tree Sparrow (*P. montanus,* Price 1979). We extracted morphological data from the literature on House Sparrows of other subspecies from Europe (Grimm 1954, Niethammer 1953, Löhrl and Böhringer 1957) and North America (Packard 1967a). From these latter papers, we also estimated geographical distance between locations for a sample of populations. Distances between four locations in Germany (Stuttgart, Leipzig, Bonn, Nordheim) were calculated for mass and wing length comparisons. In Kansas and Colorado, distances between six locations were calculated for weight comparisons, and distances between eight locations were used for wing-length comparisons.

Results.—We captured 94 House Sparrows in Saudi Arabia. Sixty were from Taif and 34 from Jeddah (Table 1). There were significant differences both between populations and sexes (Table 2). When sexes were combined, birds from Taif were about 3 g heavier and had longer wings and bills, whereas birds from Jeddah had longer tails, and deeper and wider bills. Other traits, which are less subject to diurnal and seasonal fluctuations, showed differences varying up to maximum of 12% (in bill width). Males are larger than females at both sites, especially in wing length, but all the geographical patterns are seen when each sex is analyzed separately (Table 1). The only significant sex by region interaction is in body weight.

TABLE 2

TESTS FOR DIFFERENCES BETWEEN SEXES AND REGION OF HOUSE SPARROWS FROM TAIF AND JEDDAH IN SAUDI ARABIA[a]

	Sex	Region	Sex × region
Mass	10.353**	32.168***	13.231***
Wing length	23.497***	5.857*	0.771
Tail length	8.076**	15.369***	0.016
Tarsus length	1.636	3.985*	1.848
Bill length	0.574	6.003*	0.072
Bill depth	2.952	14.749***	3.894
Bill width	0.655	53.767***	1.527

[a] F-values from two-way analyses of variance are presented, N = 94 birds. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

When compared with locations outside Saudi Arabia, sparrows from Jeddah are of strikingly low mass (Table 3). The heaviest birds are found in the locations further north, in Punjab, India (Saini et al. 1989), and in Kazakhstan (Gavrilov 1965). Differences between Jeddah and Taif populations are comparable to those among those of Kazakhstan, north India, and south India. The large differences between Jeddah and Taif are further illustrated in plots of geographical distance against weight and wing length (males only) for North America and Germany (Fig. 1). Populations in Germany show stronger differentiation than North America, but the Jeddah-Taif difference is a conspicuous outlier.

Discussion.—Vaurie (1956) divided House Sparrow populations into two groups: the Palearctic group with six races, and the Oriental group with another six races. *Passer domesticus indicus* is a member of the oriental group extending from the Red Sea in Saudi Arabia to Burma in the east (Summers-Smith 1988). Johnston and Selander (1964, 1973), in their studies of North American and European populations, showed that wing length increases with latitude and altitude in a pattern which matches that seen in Saudi Arabia. There have only been a few studies on *P.d. indicus,* all from central Asia and the Indian sub-continent (Gavrilov 1965, Gavrilov and Korelov 1968, Saini et al. 1989).

The differences we find between populations in Saudi Arabia are much larger than dif-

TABLE 3

MEAN MASSES (G) AND WING-LENGTHS (MM) OF SOME POPULATIONS OF *P. D. INDICUS*

	Males			Females		
	N	Mass	Wing length	N	Mass	Wing length
South India[a]	37	22.03	73.11	26	22.70	71.54
North-west India[b]	135	23.61	76.17	90	23.68	72.97
Kazakhastan[c]	70	24.80	76.80	—	—	—
Unknown[d]	—	27.50	74.50	—	—	76.80

[a] Price (unpublished).
[b] Saini et al. (1989).
[c] Gavrilov 1964 (data are for males and females).
[d] Summers-Smith 1988 (no location and sample size are given).

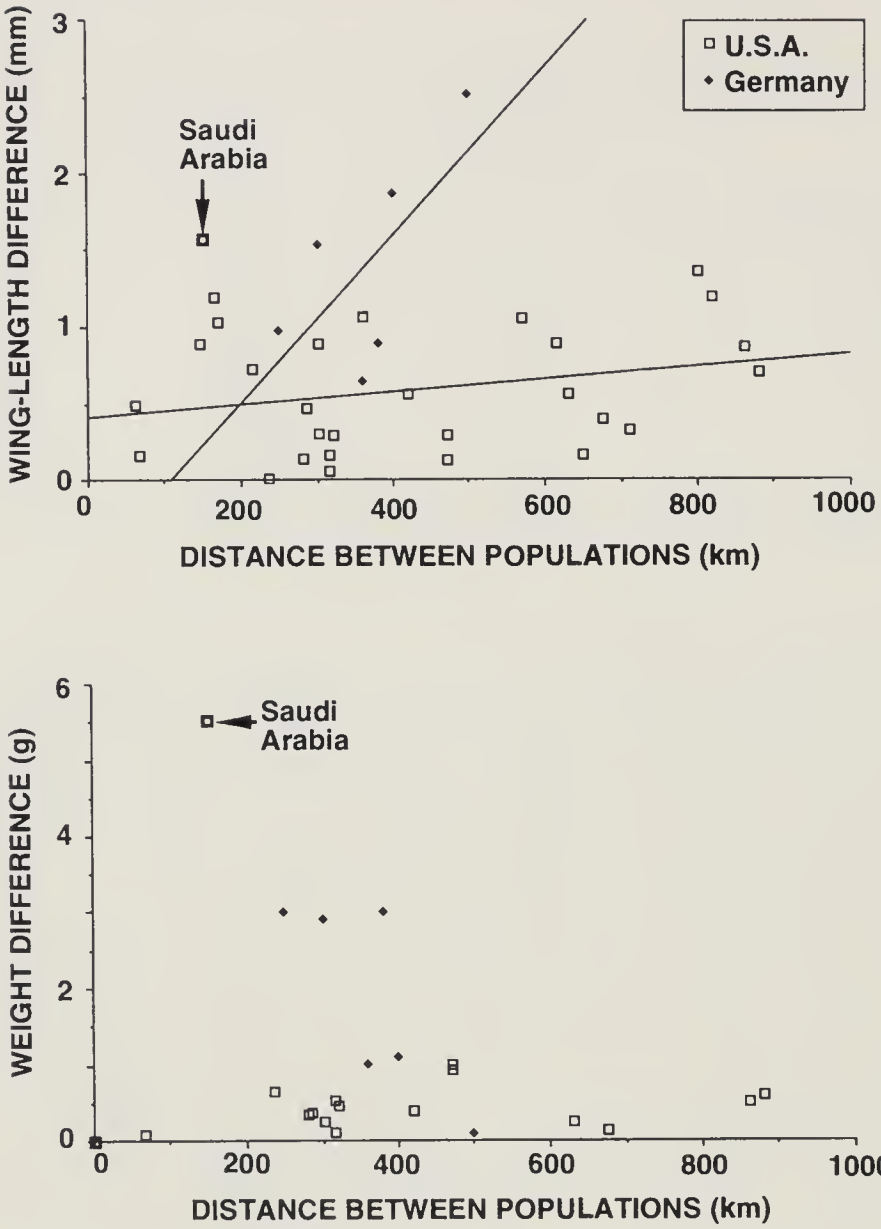

FIG. 1. Plots of differences in male wing length (above) and male weight (below) against geographical distance for Germany (Grimm 1954, Niethammer 1953, Löhrl and Böhringer 1957), North America (Packard 1967a), and Saudi Arabian populations. For wing length, lines are the least-square regression lines fit separately to the Germany and North America data.

ferences over comparable distances in Germany and the U.S.A. (Fig. 1). The large differences may be explained in two ways. First, altitudinal variation between our two sites in large, and for other species, larger birds have been shown to occur at the higher, colder altitudes (Diamond 1973, Britton 1977). Britton (1977) and Hanmer (1978) have compared weights of birds at high and low altitudes in Kenya and found striking differences among populations. The longer, thinner bills at Taif may reflect the type and availability of food in rural areas (e.g., Davis 1954, Packard 1967b, Selander and Johnston 1967). The slightly shorter tarsi at Taif run opposite to the general pattern of increased size and may reflect

foraging adaptations (Grant 1966). The second reason for the relatively large differences between populations in Saudi Arabia may be the length of time that the species has been established there. In Germany, it must have reinvaded following the last ice age and the spread of agriculture, and in North America sparrows were introduced only last century (Summers-Smith 1988, 1990).

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HASSAN M. FELEMBAN, *Dept. of Biological Sciences, Faculty of Science, King Abdul-Aziz Univ., P.O. Box 9028, Jeddah 21413, Saudi Arabia*; AND TREVOR D. PRICE, *Biology Department 0116, Univ. of California at San Diego, La Jolla, California 92093.* *Received 30 April 1996, accepted 8 Feb. 1997.*

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A female Gambel's Quail with partial male plumage.—Gambel's Quail (*Callipepla gambelii*) are sexually dimorphic, with males exhibiting head plumes that are long, wide, and black, a rusty head patch, a black facial bib outlined in white, and a black belly patch. Females have dark brown plumes which are shorter and narrower than males, and do not exhibit the other listed traits (Johnsgard 1973). In the late summer of 1996, we observed a captive female Gambel's Quail molting into partial male plumage. The female was at least two years old and had exhibited only female plumage in previous years.

We compared this female with typical male and female Gambel's quail (Table 1). The head plumes of the aberrant female were long, wide, and black, consistent with male plumes. In addition, the female had developed a striking rusty head patch. The posterior portion of the patch contained a mixture of rust and gray feathers, unlike a typical male. The female had an obvious facial bib composed primarily of beige, rather than black feathers. The white outline of the bib was present on the sides, but did not extend far down the throat. There was no black belly patch, but some black-tipped feathers were scattered throughout the belly region. A typical female has beige belly feathers with some brown streaking.

Many sexually dimorphic galliform birds, best studied in the pheasants (Phasianinae), exhibit estrogen-dependent plumage development (Domm 1939, Witschi 1961, Owens and Short 1995). Dull female plumage is dependent upon the presence of estrogen, while ornamental plumage of males develops in the absence of estrogen. This has been demonstrated experimentally, where ovariectomized females developed full male plumage. Similarly older females, or females with diseased ovaries, molt into partial or full male plumage because they do not produce sufficient estrogen. Therefore, ornamental male plumage is the "default" state in both sexes, and female plumage may be more derived (Owens and Short 1995).

The actual mechanism that disrupted normal estrogen levels in the female Gambel's Quail we observed is unknown. She had experienced no known injuries or disease while in captivity, and acted as healthy and vigorous as other females in her pen. When the female first exhibited partial male plumage, she was at least two years old, which is older than most wild females. Sowls (1960) reported an annual survival rate of only 28–40% for Gambel's Quail. Mean longevity for quail after their first fall is approximately 8–10 months (Johnsgard 1973: Table 21).

Given abnormal estrogen production in the female we observed, partial male plumage development may have occurred in one of two ways. First, feather tracts differ in their sensitivity to estrogen (Juhn et al. 1931). If this female produced low concentrations of estrogen throughout molt, male plumage may have developed in some areas that were highly estrogen sensitive, but not in others. Alternatively, estrogen may have been produced only during a portion of molt. Thus, female feathers developed when estrogen was present, while male feathers developed in the absence of estrogen.

While estrogen-dependent plumage dimorphism has been observed most in Phasianinae (Domm 1939, Witschi 1961, Owens and Short 1995), it has not been well documented in

TABLE 1
PLUMAGE CHARACTERISTICS OF GAMBEL'S QUAIL

	Typical male (N = 45)	Typical female (N = 38)	Female with male plumage
Plume length, mm[a] ($\bar{\chi} \pm$ SD)	42.1 ± 2.5	31.4 ± 1.9	42.0
Plume color	Black	Dark brown	Black
Rusty head patch	Present	Absent	Present
Black belly patch	Present	Absent	Some black-tipped feathers
Facial bib	Present	Absent	Present
Facial bib color	Black	———	Beige, some black feathers

[a] Typical male and female plumes are significantly different ($t = -24.5$, $df = 81$, $P = 0.001$).

New World quail (Odontophorinae). Domm (1939) cited unpublished data indicating ovariectomized female Northern Bobwhites (*Colinus virginianus*) developed male plumage. In addition, Crawford et al. (1987) observed a female California Quail (*Callipepla californica*) with partial male plumage in the wild.

We suggest that Gambel's Quail also exhibit estrogen-dependent plumage control. Our hypothesis is supported by experiments on male Gambel's Quail. Castrated juveniles exhibited completely normal male plumage as adults, suggesting that testosterone was unimportant in the development of male ornamental plumage (J. C. Hagelin, unpub. data). Furthermore, some females in wild Gambel's Quail populations have dark, male-like plumes that are longer than average for a female, and exhibit some male-like rusty flecking on their heads (J. C. Hagelin, unpub. data).

Our observations of Gambel's Quail, combined with data on Phasianinae (Domm 1939, Witschi 1961), one species of Old World partridge (Kannankeril and Domm 1968), and other Odontophorines (Domm 1939, Crawford et al. 1987), lends support to the idea that estrogen control of sexually dimorphic plumage is universal among galliforms. This has implications in studies of honest signaling and good genes models of sexual selection (Andersson 1994). Folstad and Karter (1992) suggested that males with testosterone dependent, secondary sexual traits may be signaling immunocompetence, because high testosterone levels negatively affect immune function. Highly ornamented plumage, however, does not reflect testosterone levels in male galliforms. Rather, it reflects a lack of estrogen. Thus, the validity of the immunocompetence handicap to explain the evolution and maintenance of the highly ornamented male plumage in the Galliformes must be questioned (Owens and Short 1995). Consistent with this hypothesis, several studies of mate choice in galliforms indicate that male plumage does not influence female choice (e.g. Buchholtz 1995; Ligon and Zwartjes 1995; J. C. Hagelin, unpub. data).

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JULIE C. HAGELIN AND REBECCA T. KIMBALL, *Dept. of Biology, Univ. of New Mexico, Albuquerque, New Mexico 87131.* *Received 22 Oct. 1996, accepted 1 April 1997.*

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Ice fishing by wintering Bald Eagles in Arizona.—Northern Arizona winters vary within and between years with occasional heavy snows (up to 0.6 m) and extreme cold (overnight lows −18 to −29°C) interspersed with dry periods, mild temperatures (daytime highs reaching 10°C), and general loss of snow cover at all but highest elevations. Lakes in the area may freeze and thaw partially or totally several times during a winter. The freezing and thawing of 1000-ha, 2-m deep Mormon Lake, 34 km south of Flagstaff, Arizona, during the winter of 1994–95 set the stage for the unusual Bald Eagle (*Haliaeetus leucocephalus*) ice fishing behaviors we describe.

Traditional ice fishing.—We here use "traditional" in the anthropomorphic sense, i.e., breaking a hole in the ice and waiting for fish to come within striking distance. On 22 Dec. 1994, when Mormon Lake was 100% frozen over from an early cold spell, we observed an adult Bald Eagle land near shore and begin intermittently jumping up and down on the ice for about 1 min. It broke the ice creating a 0.6-m diameter opening without falling into the water. Then it flapped onto an unbroken edge. It removed a chunk of ice from the opening with its foot, before moving 2 m away to stand among emergent reeds (*Carex* sp. and *Juncus* sp.). After about 2 min, the eagle hopped to the open water hole, grabbed a 10-cm (estimated) fish, and flew back to the reeds to feed. After four head-to-foot feeding movements, the adult was flushed by a second adult and an immature eagle landing nearby.

Subsequently, between 2–8 February 1995 when Mormon Lake was again 70–95% fro-

zen, we had corroborating observations of two adult eagles breaking holes in the ice four times and four immature eagles jumping into existing holes five times. Three of these efforts resulted in prey capture and feeding (overall success including initial observation, 40%). We saw no immatures create their own fishing holes. This type of foraging was uncommon and limited to conditions of thin ice in near-shore shallows (<0.3 m). Inadvertent breakthroughs that also occurred on thin ice during landings were readily differentiated from intentional ice breaking. Eagles showed no interest in such spots, usually appeared startled, and upon regaining their balance, quickly flew away with no evidence of prey.

Ice scavenging.—When Mormon Lake froze shore-to-shore in December 1994, there was an extensive die-off of fathead minnows (*Pimephales promelas*), an introduced bait species which had been flourishing since a 1990 drought. As the lake thawed and refroze through January 1995, dead minnows were caught in the surface ice. By early February, we observed large numbers of both adult and immature Bald Eagles (>100) scattered on the lake ice along with small groups of Common Ravens (*Corvus corax*) picking minnows out of the frozen surface. Foraging was characterized by an occasional peck at the ice and/or a single head-to-foot movement. Also, there were no antagonistic interactions between foraging eagles. All three behaviors indicated small, "one-bite" prey. Except under ideal lighting conditions, we rarely were able to see the 4–6-cm minnows from our vantage points 0.4–0.8 km away. Positive identification was possible only after a visit to the lakeshore ice. Occasionally foraging eagles would grasp minnows in their talons and make a short flight before landing to eat. Ice-scavenging eagles consistently moved around on the frozen lake, but there was always more idle standing than either active foraging or flying.

Small-hole scavenging.—Another visit to the lakeshore ice in mid-February revealed a third unusual foraging behavior involving 3–5-cm holes and the plentiful fathead minnow carcasses. Walking near shore on the 7.5-cm thick ice where a dozen eagles had been earlier, we were surprised to find no minnows on the surface. Instead, we found numerous small holes where emergent twigs and vegetation were growing in the shallow water (<0.5 m deep) and protruding through the ice. Apparently because of wind and wave action, ice immediately around stems was less than 2.5 cm thick. Most holes were centered on a stem; however, small ice chips scattered around the holes indicated they had been actively chipped out and did not form naturally. Approximately 30% of the holes had minnows floating in them, many with multiple carcasses. Two species of small (approximately 1-cm diameter), dead, freshwater snails (*Planorbella tenius* and *Physa virgata*) were also floating in some of the holes. In addition, we discovered minnows were visible floating up under the clear, unbroken but thinner, ice surrounding stems.

Although we could never discern Bald Eagles chipping these scavenging holes, we believe they did so because they were the only species consistently seen near the holes during our extensive observations. We hypothesize that as minnows frozen in the ice surface were depleted and as the foraging surface melted, scavenging eagles turned to the remaining shoreline ice and chipped holes with their beaks where they could see dead minnows floating up under the surface. Between 12–17 February, we recorded at least six adult and six immature eagles pulling minnows and/or snails out of small holes in the ice. They either reached down and grabbed the prey in their beaks, flap-hopped above the hole and grabbed the item in their talons, or used a combination of both techniques. Some eagles moved rapidly from hole to hole, consuming as many minnows as possible, while others defended preferred foraging spots.

Walking on the relatively thin ice, we found our movements and body weight caused water and often accompanying minnows to squirt out of nearby scavenging holes. Apparently, eagles discovered this same phenomenon, perhaps when trying to grab prey items with their talons. On 17 February, we observed two adults and two immatures separately

and repeatedly hopping up and down near scavenging holes. These individuals normally walked to an opening, ate, and moved on. But if unsuccessful, they might poke at a hole with their beaks four-to-five times, try the hole with their talons one to two times, then simply hop up and down in the same area two-to-three times, until finally they were able to grab a minnow out of the target hole.

Temporal foraging perches.—The last form of "ice fishing" was more subtle than the previous behaviors, yet it enabled wintering Bald Eagles to use prey and habitat that might not have otherwise been accessible. By mid-February, Mormon Lake was 95% ice-free during daylight hours. However, on typically calm, cold nights, a smooth, thin sheet of ice formed across the lake surface. On calm days it would persist until mid-day. The temporary but recurring ice was sufficient to support foraging Bald Eagles among the numerous emergent patches of marsh grass (*Scirpus* sp.) scattered across the lake. During early morning hours, most eagles at Mormon Lake were out on the ice among these grasses. Landing eagles often slid on the smooth surface and frequently broke through the thin veneer, but otherwise there was no indication of the unexpected circumstance facilitating their foraging among the clumps of marsh grass.

On 14 February at 09:50 MST, we recorded 18 adults and 59 immatures on the morning lake ice. By 16:00, only 23 eagles remained around the entire lake shore. None was seen among the marsh grass, where most had been in the morning and where no ice remained. The value of temporal ice became evident when we discovered the water depth at these clumps of marsh grass consistently exceeded 1 m, well beyond wading depth for Bald Eagles. Yet, scavenging eagles were able to take advantage of dead minnows and small snails caught down among, or living on, the emergent grasses, which otherwise blocked normal aerial foraging on these prey items when no ice was present. Foraging among these grasses consisted of individuals slowly walking around, looking down at the ice surface and/or vegetation, and occasionally bending down to pick up very small prey items, which we suspected were most often snails from their abundance and size. This is the second documented occurrence of eagles in the area feeding on molluscs. In 1978, Bald Eagles wintering at Lake Mary (10 km north of Mormon Lake) foraged on freshwater mussels (*Anodonta corpulenta*; Grubb and Coffey, Wilson Bull. 94:84–85).

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Teryl G. Grubb and Roy G. Lopez, *USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 2500 S. Pine Knoll Drive, Flagstaff, Arizona 86001-6381.* *Received 2 Dec. 1996, accepted 27 Feb. 1997.*

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ORNITHOLOGICAL LITERATURE

EDITED BY WILLIAM E. DAVIS, JR.

EXXON VALDEZ OIL SPILL: FATE AND EFFECTS IN ALASKAN WATERS. Edited by Peter G. Wells, James N. Butler, and Jane Staveley Hughes. American Society for Testing and Materials, Philadelphia, Pennsylvania. 1995: ASTM Special Technical Publication 1219, 955 pp., introduction, 25 technical papers, author and subject indices. $55.00 (cloth).—This volume contains some of the papers presented at the Third Symposium on Environmental Toxicology and Risk Assessment held in Atlanta, Georgia on 26–28 April 1993. Most of the research reported in this volume was supported by the Exxon Company, USA, during the period 1989–1991, following the grounding of the T/V *Exxon Valdez* in Prince William Sound, Alaska, on 24 March 1989. The accident resulted in the release of an estimated 11 million gallons of crude oil from Alaska's North Slope into the sound; some of this oil was—and still is—deposited on beaches as far as 900 km to the southwest.

One of the truths of the *Exxon Valdez* oil spill (hereafter, EVOS) is that there is no single version of what happened, particularly in regard to long-term effects. My own perspective is that of someone who works for the state-federal EVOS Trustee Council, which was appointed to administer the damage assessment and restoration programs following the spill. The following comments reflect my own views and not those of the Trustee Council.

The Atlanta symposium was the first forum for public discussion of results from Exxon's post-spill science program. Exxon's contractors were invited to participate in a Trustee Council-sponsored symposium in Anchorage, Alaska on March 1993, but none presented papers. Several Trustee Council-sponsored investigators participated in the Atlanta symposium, but only one of their papers appears in this volume (McDonald et al., pp. 296–311). Proceedings from the Trustee Council symposium are now available as well (Rice et al. 1996). Together, these books frame the issues regarding initial and short-term (i.e., 1–3 y) injuries. As the results of the Exxon- and Trustee Council-sponsored studies find their way into the open literature and follow-up studies are conducted, there will be ample opportunity for contrast and synthesis.

Following an introductory chapter, "Introduction, Overview, Issues" (Wells et al., pp. 3–38), this volume is organized into sections on the "Chemistry and Fate of the Spill" (6 papers), "Shoreline Impacts of the Spill" (6), "Impact Assessment for Fish and Fisheries" (4), "Impact Assessment for Wildlife" (8), and "Impacts on Archaeological Sites" (1). The introduction is largely a summary of the contents, but the editors comment more broadly on lessons learned from EVOS. Their bottom line is that chronic effects of the spill on wildlife and fisheries are limited and, at the population level, blend with natural factors, resulting in variability in the abundance and distribution of species. An assertion that Exxon's studies, but not those sponsored by the Trustee Council, are "synoptic, covering unimpacted as well as impacted areas" (p. 6) is wrong. From the outset, studies sponsored by the governments made ample, contemporaneous use of unimpacted areas as reference sites (e.g., EVOS Trustee Council 1989).

The balance of this review addresses the bird studies in the "Impact Assessment for Wildlife" section. My intent is to highlight some of the issues for readers who plan to wade into the now burgeoning EVOS literature.

The paper by Day et al. (pp. 726–761), "Use of Oil-Affected Habitats by Birds After the *Exxon Valdez* Oil Spill," is innovative because it assesses impacts on and recovery of the birds' use of oiled habitats rather than the birds themselves. This approach complements

that of the Trustee Council-sponsored boat surveys, which drew on limited historical data to look at impacts to and recovery of bird populations (e.g., Agler et al. 1994, Klosiewski and Laing 1994). Looking at the Exxon and Trustee Council surveys together, there is agreement that there were impacts with respect to several bird species, including, for example, Black Oystercatchers (*Haematopus bachmani*) and Harlequin Ducks (*Histrionicus histrionicus*) in Prince William Sound.

Day et al. defined impact as "a statistical difference in the abundance of a species among bays exposed to various levels of oiling, after habitat differences . . . have been taken into account" (p. 728). Recovery is achieved when a significant difference is no longer evident. Of course, not finding a difference can reflect either a real lack of difference or a lack of sufficient statistical power to detect a difference if one should exist. Day et al. present no analysis to quantify the latter, but their use of alpha levels of up to 0.20 increased the chance of detecting oiling effects.

The approach taken by Day et al. enabled the conclusion, for example, that in 1989 there was an initial, early-summer impact on Marbled Murrelets (*Brachyramphus marmoratus*), but that recovery in the use of oiled habitats was achieved by mid-summer of the same year. This tells us something about how quickly birds can reoccupy oiled marine habitat, but it reveals little or nothing about impact on or recovery of the murrelets themselves. I am not persuaded that reoccupancy of an oiled habitat necessarily is a "clear sign that . . . other types of recovery [demographic and reproductive . . .] can proceed" (p. 728). It is entirely possible that birds continue to use polluted habitats that are detrimental to short- and long-term survival and productivity. Day et al. twice cite Morrison (1986) in support of the idea that reoccupation means that recovery can proceed, but Morrison did not address this issue. In fact, the thrust of Morrison (1986) is that birds are not effective environmental indicators.

Two papers address the status of murres (Common, *Uria aalge,* and Thick-billed, *U. lomvia*), which accounted for 74% of the oiled bird carcasses recovered following the spill (Piatt et al. 1990). Exxon's approach to the issue of impacts on murres was (1) to compare their post-spill surveys of murres at colonies in the oil-spill area with historical data and the Trustee Council's post-spill surveys, and (2) to conduct more intensive studies on numbers of murres and productivity at one of two colonies in the Barren Islands, lower Cook Inlet.

Erikson (p. 780–819), "Surveys of Murre Colony Attendance in the Northern Gulf of Alaska Following the *Exxon Valdez* Oil Spill," takes the first approach and concludes that impacts on murre colony attendance were relatively short-term. Post-spill colony attendance estimates in 1991 by both Erickson and U.S. Fish and Wildlife Service staff (Nysewander et al. 1993a) were similar, giving some confidence that both sets of biologists can count murres! The real issue is how one interprets historical data in relation to these post-spill colony estimates.

Erikson points out the difficulties in estimating colony attendance and the errors in the historical data in the "Catalog of Alaskan Seabird Colonies" (USFWS 1991), but he was uncritical in selecting only the most recent counts for comparison in his test for a change in numbers caused by oiling. For example, without an accompanying note (Table 3, p. 800), Erikson used counts within the Chiswell Island group by Nishimoto and Rice (1987) that were obtained under marginal sea conditions. These counts were low relative to earlier counts by Bailey (1976), thus giving the impression of little change in pre- and post-spill numbers in the Chiswell I. The best approach might have been to conclude that neither set of counts provided a good basis for comparison.

Beyond the issue of which historical estimates are most appropriate, Erickson assigned murre colonies to risk categories (high, moderate, and low) depending on colony location

relative to the oil. Since "the pelagic distributions of murres for the individual colonies is not known" (p. 786), however, these categorizations and the related ANOVA analysis are problematic. For example, colonies separated by only a few km are assigned different risks (e.g., Chiswell I.-high; Rugged I.-moderate), even though such distances are well within likely foraging ranges of birds attending colonies (Ainley and Boekelheide 1990), and murres on the water in the pathway of the spill may not yet have moved into colonies nearer shore (e.g., Rugged Island).

The most important group of murre colonies in the spill area is in the Barren I. The paper by Boersma et al. (p. 820–853), "Common Murre Abundance, Phenology, and Productivity on the Barren Islands, Alaska: The *Exxon Valdez* Oil Spill and Long-Term Environmental Change," again underscores the importance of the interpretation of historical data.

In Table 2 (p. 833), Boersma et al. present a confusing array of historical murre estimates—including preliminary and final estimates and even numbers acknowledged to be in error—from East Amatuli I.-Light Rock in the Barren I. group. For example, two estimates for Light Rock in 1978 consist of a preliminary estimate of 10,000–30,000 murres (Simons and Pierce 1978) and a final estimate of 20,000 that Manuwal (1978) derived from his field assistants' (Simons and Pierce 1978) preliminary figures. Why are these numbers presented? On the one hand, Boersma et al. use them to illustrate the poor quality and unreliability of the historical data. On the other hand, they use these data to show that their estimates of about 35,000 murres at East Amatuli I.-Light Rock during 1990–1992 fall within the range of pre-spill, historical estimates for the Barren I. Unfortunately, the historical range they proposed, 19,000–61,000, mixes an apple and an orange. The "apple" is the figure of 19,000, which was not reported by Manuwal (1978) and which Boersma et al. referred to as a "presumed" count (p. 843). This number must have been calculated from Simons and Pierce's (1978) preliminary estimate for birds on the cliffs at Light Rock and a number that was apparently doubled by Simons and Pierce to account for murres on the cliffs and at sea at East Amatuli I. The "orange" is Bailey's (1976) figure of 61,000, which was an attempt to estimate the total population of the East Amatuli I.-Light Rock colony by counting birds on the cliffs and water and in the air. The bottom line is confusion, and my conclusion is that the historical data do not provide a reliable basis for interpretation of post-spill estimates.

Boerma et al. question some of the early conclusions that the oil spill disrupted reproductive timing and synchrony in murres in the Barren I. (e.g., Nysewander et al. 1993b). I agree with them and so do Piatt and Anderson (1996). The case presented by Boersma et al., however, is less than compelling, since it is based on work at only one of the two Barren I. colonies (East Amatuli I.-Light Rock); and, within that one colony, their study focused on a single 5 × 5 study plot on a flat area of optimum habitat on top of Light Rock that is strikingly different from the narrower rock ledges on vertical cliffs on which most murres nest in the Barren I (D. Roseneau, pers. com). Finally, Boersma et al. do not address evidence of disruption of breeding murres at other colonies, such as at Puale Bay on the Alaska Peninsula (e.g., McCarthy and Dewhurst 1993).

Stubblefield et al. (pp. 665–692) present an "Evaluation of the Toxic Properties of Naturally Weathered *Exxon Valdez* Crude Oil to Surrogate Wildlife Species" and conclude that the exposure concentrations observed in Prince William Sound after 1989 would present negligible toxic risk to wildlife. The Mallard (*Anas platyrhyncos*) was their avian surrogate for a battery of tests for acute and subacute toxicity, but there was no discussion of whether Mallards in laboratories are good surrogates for Harlequin Ducks and other birds in harsh marine habitats. Holmes et al. (1979) established that under sheltered laboratory conditions Mallards can ingest large amounts of petroleum without showing signs of distress, but that mortality frequently occurred among Mallards subjected to even small environmental stress-

es (e.g., sustained mild cold). Stubblefield et al. do not cite this highly relevant paper (Holmes et al. 1979), nor did their tests include environmental stresses on the surrogates.

White et al. describe the "Density and Productivity of Bald Eagles [*Haliaeetus leucocephalus*] in Prince William Sound, Alaska, After the *Exxon Valdez* Oil Spill" (pp. 762–779). Their message is that there were no demonstrable effects of the oil spill on eagle density or reproduction one and two years after the spill. This agrees well with Bowman et al. (1995): Their surveys documented an initial impact on Bald Eagles, but they predicted recovery by 1992. Indeed, the Trustee Council listed the Bald Eagle as a "recovering" species in its restoration plan (EVOS Trustee Council 1994).

Wiens (pp. 854–893) concludes this volume's bird papers with a chapter on the "Recovery of Seabirds Following the *Exxon Valdez* Oil Spill: An Overview." He starts by noting that early concerns expressed by Trustee Council-sponsored investigators and others about the initial impacts of the spill on birds and predictions of extended recovery times "were not based on careful, scientific studies . . ." (p. 857). This is puzzling given that one of the most prominent, early predictions—that Common Murres might require recovery times of 20 to 70 years, or sooner (Piatt et al. 1990)—was in large measure based on modeling work by Wiens and his students (Ford et al. 1982).

Wiens proposes that if injury cannot be detected statistically, then no injury has occurred; recovery is the disappearance through time of statistically significant differences between oil-exposed and reference samples. The no-significant-effect-means-no-effect-existed contention is logical when data are ample, but the absence of a significant effect may reflect nothing more than the lack of sufficient power to detect an effect, which is often the case in view of limited historical data, natural variations in populations and productivity, and complicated interpretation of results at off-site controls. Peterson (1993:36) refers to the contention that no significant effect means no effect existed as a "recurring fallacy" and suggests that, in the absence of convincing analysis of power, definitive conclusions about no effects are unjustified.

Wiens begins a discussion of equilibrium and natural variation by noting that "recovery is often thought to have occurred when the system returns to its state before a disruption, such as an oil spill" (p. 862). This is something of a red herring in regard to EVOS. The federal Natural Resources Damage Assessment regulations (43 CFR, Subtitle A, Part 11) that served as an initial framework for the *Exxon Valdez* damage assessment make clear that recovery means a return to baseline conditions that would have existed had the spill not occurred--quite a different concept from the one Wiens describes. In the subsequent restoration program, pre-spill conditions are used as proxies because of the difficulty in predicting the conditions that would have existed had the spill not occurred. Further, there is explicit recognition that, in the case of species that had declined before the oil spill (e.g., Marbled Murrelet and harbor seal [*Phoca vitulina*]), this objective is not realistic (EVOS Trustee Council 1994).

Wiens criticizes Laing and Klosiewski's (1993) boat surveys in Prince William Sound for basing their comparisons of pre- and post-spill data "on the premise that differences in the state of the system before and after the spill are due to spill effects alone" (p. 867). This is incorrect: Laing and Klosiewski (1993; also Klosiewski and Laing 1994) also test whether marine bird populations in the oiled zone of Prince William Sound were less than expected given the pre-to-post-spill changes that had occurred in the unoiled zone, thus employing both geographic and temporal controls.

Wiens wonders why there are disagreements about the effects of EVOS and suggests that some studies, presumably those sponsored by the Trustee Council, focused on damages, while others, presumably Exxon's, also included recovery. To be sure, the studies sponsored by the Trustee Council during 1989–1991 were part of an injury assessment for the purpose

of presenting a damage claim to the spillers of the oil, but determining the extent and rate of natural recovery of injured resources was integral to the process from the outset (e.g., EVOS Trustee Council 1989). Is it unfair to assume that the only reason that Exxon's studies emphasized recovery was to limit the legal and economic liability of the corporation? Perhaps, but it is even more unfair to imply that the governments' only interest was in documenting injury when the determination of recovery is essential to ecologically and commercially important management decisions and to organizing a restoration program (e.g., Strand et al. 1993).

Determining the biological significance of impacts and distinguishing between natural variation and spill effects are key themes in Wiens' paper. These themes are relevant, but I caution readers to be aware of what Peterson (1993:33) called the "fallacy of natural variation," in which it is inappropriately argued that because an impact is small in magnitude relative to the natural range of variation the impact is of no ecological consequence. Wiens does not discuss whether mortalities to birds from oil spills or other anthropogenic perturbations are additive or compensatory (e.g., Piatt et al. 1991) or the possibility of interactive, cumulative effects on populations (e.g., Ainley and Lewis 1974, Ainley and Boekelheide 1990). A series or combination of natural and anthropogenic events can reduce a population's natural resiliency, and, whatever the effects of EVOS were, they were superimposed on a decadal-scale period of change and decline for an entire suite of fish-eating marine birds and marine mammals in the north Pacific (e.g., Duffy 1991, Piatt and Anderson 1996). The interaction of spill effects and natural environmental change may be the long-term legacy of this oil spill.

In sum, this volume of mostly Exxon-sponsored reports is an early contribution to the scientific literature on EVOS effects. Readers should approach this volume with caution and an open mind, just as they should approach reports on research sponsored by the Trustee Council. The comments offered above are intended to flag some of the issues to consider as this story unfolds over the next decade or more. Thanks are due to the following individuals who either read a draft of this review or otherwise provided assistance: V. Byrd, C. Haney, D. Irons, M. Morrison, C. Peterson, J. Piatt, B. Rice, S. Rice, D. Roby, D. Roseneau, J. Senner, R. Spies, B. Wright, and an anonymous reviewer.—STANLEY E. SENNER

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NEARCTIC PASSERINE MIGRANTS IN SOUTH AMERICA. By Raymond A. Paynter, Jr. Publication of the Nuttall Ornithological Club, No. 25, Cambridge, Massachusetts. 1995: 126 pp., X + 72 range maps, 3 tables, $13.50 (cloth).—The tremendous recent surge of interest in the conservation of nearctic passerine migrants (or neotropical migrants, as they are more often called) has focused overwhelmingly on north temperate breeding grounds and wintering areas in Central America and the West Indies. This focus reflects the geographical distribution of scientists, the ease of reaching study areas, and greater abundance of migrants in Central America and the West Indies. As a result, we know very little about the distribution of migrants in South America, even though 68 passerine species winter on the continent. The species that winter mainly in South America include some species identified as being of high priority for conservation because of population declines and habitat loss, including the Olive-sided Flycatcher (*Contopus borealis*), Cerulean Warbler (*Dendroica cerulea*), Canada Warbler (*Wilsonia canadensis*), and Bobolink (*Dolichonyx oryzivorus*). Migrants such as swallows, Swainson's Thrushes (*Catharus ustulatus*) and Eastern Kingbirds (*Tyrannus tyrannus*) are abundant and conspicuous members of the tropical communities in which they winter. Before we can evaluate the extent to which these species are threatened by wintering ground habitat loss, we need better information on their winter ranges and habitat requirements.

The goal of this book is to provide range maps showing where each species occurs in South America. The range maps are based on a review of more than 500 publications (on file at the Museum of Comparative Zoology, Harvard University) on bird distribution at 1,260 different sites. The maps show the exact locations (points) at which a bird is known to have been collected and/or observed. No data are provided on abundance, habitat, or date of observation for each point. The text accompanying each species, however, usually attempts to summarize the seasonal pattern of occurrence, the general habitats occupied, and the abundance in different regions. The introductory section is brief (5 pages) and there is a concluding section on general patterns of distribution, relative abundance, and summer residents.

The book succeeds in providing useful data for conservation planners. The greatest concentration of migrants is in the Northern Andes region where human population pressure is great and habitat loss is proceeding rapidly. Many of the migrants in this region include such declining species as the Olive-sided Flycatcher and the Cerulean and Canada Warblers. The data in this volume lend support to the hypothesis that winter habitat loss is a particularly likely cause for their population declines.

One of the major limitations of this volume is the lack of data on the dates of occurrence for each point. As a result, it is difficult to determine which records likely pertain to passage migrants and which refer to locations where the species truly "winters." This is an especially severe problem with relatively late migrants such as the Veery (*Catharus fuscescens*), which is usually depicted as having a large winter range, but may in fact winter in only a small part of Southwestern Amazonia (J. V. Remsen, pers. comm.). The species accounts usually mention locations where the species may be just a passage migrant, but it would have been useful to have dates, or at least months, of collection or observation on the maps. Similarly, a more detailed map of South America showing the Andes would have helped readers interpret the winter ranges.

Based on my own experience, which is mostly in southeastern Peru, I found the maps to be generally accurate. There is a point missing for the Connecticut Warbler (*Oporornis agilis*) from the Manu National Park, but all other species that occur there are documented by point on the range map. I can envision many tropical ornithologists looking at these range maps and noticing other gaps; this should spur many of us to publish our distributional records in a more timely manner. Paynter argues that these maps provide the broad outline and that only the details will change as more data arrive. Perhaps he is correct, other than the need to separate migratory and wintering distributions for some species.

The book is restricted to passerine migrants, which includes most, but not all terrestrial migrants. The two *Coccyzus* cuckoos, Yellow-billed (*C. americanus*) and Black-billed (*C. erythropthalmus*), also winter mainly in South America, as do several raptors. The volume therefore is not a comprehensive coverage of terrestrial nearctic migrants, nor is it intended to be.

The concluding sections of the book provide syntheses of the data, including species diversity from each country, an exploration of vagrancy in nearctic migrants, a brief mention of habitat requirements, and extensive discussion of occasional breeding by nearctic migrants in South America. Paynter argues that distributions are well defined in spite of vagrant records. Many of the species listed winter primarily in Central America and the West Indies and occur only as stragglers in northwestern Columbia or along the Caribbean Coast.

This book is a bargain at only $13.50, as are most of the volumes in the Nuttall Ornithological Club Series. It will serve as a valuable reference for the growing community of biologists who are using nearctic passerine migrants to help direct conservation strategies in South America.—SCOTT K. ROBINSON

THE ECOLOGY OF MIGRANT BIRDS: A NEOTROPICAL PERSPECTIVE. By John H. Rappole. Smithsonian Institution Press, Washington, D.C. 1995: xvii+ 269 pp., 18 figures, 27 tables, 5 appendices. $35.00 (cloth).—The main purpose of this timely book is to argue that nearctic-neotropical migrants (hereafter "neotropical migrants") are essentially tropical birds that leave the neotropics only to breed. Rappole's book is intended to counter the belief, which he feels is general, that neotropical migrants are different from neotropical residents and, therefore, have different conservation needs, at least within the Neotropics. In a parallel vein, Rappole argues that migrants also form an integral part of bird communities during migration and have special conservation needs during these periods as well. Rather than viewing neotropical migrants as supreme generalists capable of exploiting a wide range of habitats and foods, Rappole believes that many species are nearly as specialized as tropical residents and fit well into tropical bid communities. This view again runs contrary to the view that migrants are opportunists that skim the surplus resources from the margins of habitats.

Rappole offers the following general lines of reasoning to support his main thesis. (1) Many studies have shown neotropical migrants defending territories in the interior of forest habitats and may even have displays adapted specifically for winter territorial defense. (2) Some species decline after tropical forest clearing. (3) Many individuals are forced to use marginal habitats such as early second-growth because they are competitively excluded from superior forest habitats. (4) Some species are less abundant in small tropical forest fragments. (5) Wandering, nonterritorial birds may experience higher mortality rates. (6) The diets of temperate and tropical birds are generally similar. (7) There are many "floaters" in winter. (8) Migrants show comparable or even greater site fidelity to winter quarters than to breeding territories. (9) Migrants are not necessarily subordinate to residents and those that are subordinate have not been proven to suffer reduced fitness consequences. (10) Many tropical fruits are exploited by and may even be coevolved with migrants. (11) Available evidence suggests a likely tropical origin of most neotropical migrants.

Rappole also identifies and tries to refute several lines of evidence that might support different views of the ecology and evolution of neotropical migrants. (1) He argues that studies showing migrants concentrating in second/growth edge habitats are methodologically flawed (e.g., overreliance on mist nets) and ignore the birds that do defend territories in forest. He mentions only briefly that most of these studies are from Panama and South America where neotropical migrants may really be a marginal part of forest communities. I doubt if anyone would argue that neotropical migrants play a major role in forest bird communities in the northern Neotropics where Rappole has done most of his work. (2) Studies showing migrant tolerance of very small fragments are again methodologically suspect and ignore the fact that some species are less abundant in small fragments. Rappole's best example is for flocking species such as the Black-and-white Warbler (*Mniotilta varia*), which avoids fragments that are too small to sustain stable flocks. (3) Arguments that the plumage dimorphism of most neotropical migrants is an adaptation for breeding grounds ignore the possibility that winter territoriality also plays a role, as Rappole advocates. (4) If neotropical residents and migrants differ in diet, then Rappole's central thesis may be suspect. Rappole, however, argues that there is tremendous dietary overlap, even though his data here (pp. 29–30) are anecdotal. It is too bad that Poulin and Lefebvre's (1995, Auk 113:277–287) data showing huge differences between the diets of migrants and residents weren't available. These data suggests that migrants consume prey items ignored by most residents (e.g., ants); therefore, even territorial species may be exploiting "marginal" foods. Similarly, the remarkably specialized diets of many tropical birds are not mentioned. (5) Rappole emphasizes the huge geographical differences between New World and Old World migration systems, which may explain why palearctic migrants, at least in Africa, occupy marginal habitats rather than the forest interior. He further argues that the studies showing palearctic migrants as peripheral members of communities are too localized in equatorial West Africa to be generalized over a large geographical area. (6) If migrants are different morphologically from tropical residents, then they may be better adapted to exploit temperate resources. Rappole argues that support for this thesis is flawed because it fails to control for phylogeny and the possibility that tropical birds adapted to exploit the dominant temperate insect resources (especially caterpillars) are the ones that would be most likely to evolve migration.

Central to Rappole's book is the hypothesis that neotropical-nearctic migrants have a tropical origin. He argues that forced dispersal from saturated tropical habitats would inevitably lead to the evolution of migration. This argument occupies most of Chapter 6. Personally, I found his argument to be reasonable, but then again, I do not view the evolution of migration as particularly surprising in a strongly seasonal world and the high mobility

of birds. Being able to fly makes birds ideally suited to exploit temporally and spatially variable resources, regardless of their place of origin.

Rappole's central arguments have profound implications for conservation strategies, which are the focus of Chapters 8 and 9. If, as earlier argued, migrants are specialists on breeding, migratory, and wintering grounds, then they should be even more vulnerable to catastrophic habitat loss than residents. Rappole used a probabilistic model (page 137) to argue that they are roughly three times more likely to become extinct because catastrophic events can hit them at three different times and places (breeding, wintering, and stopover habitats). If, on the other hand, migrants are adaptable generalists with enormous global populations, then they are less likely to be affected by any one catastrophic habitat alteration. Similarly, if neotropical migrants are an integral part of tropical bird communities, then they may be good indicators for tropical conservation in general. If, on the other hand, they are mostly marginal members of bird communities, then they may be poor indicators for designing strategies for tropical bird community conservation. This latter view would lead to an emphasis on improving habitat for migrants in heavily agricultural landscapes, rather than saving tropical forests.

Rappole clearly recognized the importance of his central thesis, which may explain the overall tone of urgent advocacy. Rappole and his "group" (he often uses "we" in the text rather than the "I" pronoun more traditional in a single-authored book) have long advocated that conservation of neotropical migrants must first deal with tropical habitat alteration. For readers who share this view, this book will serve as a good, well-written review of the arguments in favor of this thesis. This book is also an excellent summary of the work of Rappole and his group.

For readers with different views, however, I doubt that this book will change their minds. There are too many gaps in the literature covered and oversimplifications of opposing views. The many papers showing relative insensitivity to habitat alteration in the tropics are ignored or selectively reviewed to emphasize the few species that were negatively affected. Methods of studies with opposing views are routinely challenged, but when the same methods are used to support Rappole's thesis (e.g., BBS, mist nets), they are accepted. The theory of the tropical evolutionary origin of migration ignores the likelihood that once migration has evolved, selection will continue to favor life-history and morphological traits that might lead to fundamental differences between migrants and residents.

In summary, Rappole's book will probably be cited as advocacy for the "tropics-first" view of neotropical migrant conservation rather than as a balanced review. This is partially appropriate, but it may lead readers to overlook the stimulating, but somewhat tangential sections on plumage evolution (pp. 19–21), GIS applications (p. 26), postbreeding ecology (pp. 77–78), habitat selection during migration (p. 97), austral migration (pp. 99–100), and pollution (p. 158). Perhaps time will vindicate Rappole's view; Table 9.3 provides hypotheses about which species will decline based on habitat alteration in the Neotropics.—SCOTT K. ROBINSON

THE BREEDING BIRDS OF QUÉBEC: ATLAS OF THE BREEDING BIRDS OF SOUTHERN QUÉBEC. By J. Gauthier and Y. Aubry (eds). Province of Québec Society for the Protection of Birds, Canadian Wildlife Service, Environment Canada, Québec Region, Montreal. 1996: 1302 pp., many color and black-and-white photographs $149.95.—This book is incredible. Not only is it the largest book in my library (it is 28 × 32 cm and must weigh 4 kg), but it has amazing content. Every page is packed with details, many of which are useful to readers not associated with Québec. Pages on breeding distribution are models of efficiency in

presentation of a vast amount of data. The pictures are many and generally attractive. The range maps, descriptions of species, and biological information are all detailed and well done. The book contains great maps, beautiful satellite photos of the entire province, and a truly remarkable literature section. That the editors were able to bring all of this material together is a tribute to their skills in coordinating the efforts of an extremely large group of skilled ornithologists. Be sure to see a copy of this book because it must be seen to be believed.—C. R. BLEM

HANDBOOK OF THE BIRDS OF THE WORLD. VOLUME 3: HOATZIN TO AUKS. BY J. DEL HOYO, A. ALLIOTT AND JORDI SARGATAL (EDS.). Lynx Edicions, Barcelona, Spain. 1996:821 pp., 60 color plates, many color photographs $175.—There are so many things to like in this series that it is difficult to single out one feature. The illustrations are wonderful and the photographs generally sharp and informative. The text is a concise, rich lode of information. The bibliography is well researched and detailed. I had to search closely for something to criticize. For example, occasional pages are printed less boldly than the others and I think some of the wording in picture legends is not as accurate and succinct as it could be. Both of these observations are "picky"—they take little from the overall quality of the presentation. Skip a few lunches or movies and invest in this series if you are seriously interested in birds.—C. R. BLEM.

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Editor Charles R. Blem
Department of Biology
Virginia Commonwealth University
816 Park Avenue
Richmond, Virginia 23284-2012

Editorial Board Kathy G. Beal
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Frontispiece. Taxa of the genus *Spindalis*. Left side, top to bottom: *S. zena pretrei* male, *S. z. salvini* male, *S. z. pretrei* female, *S. z. zena* female, *S. nigricephala* male. Right side, top to bottom: *S. z. benedicti* male, *S. z. townsendi* male, *S. z. zena* male, *S. portoricensis* female, *S. portoricensis* male, *S. dominicensis* female, *S. dominicensis* male. Painting by Kristin Williams.

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TAXONOMY OF THE STRIPE-HEADED TANAGER, GENUS *SPINDALIS* (AVES:THRAUPIDAE) OF THE WEST INDIES

O. H. GARRIDO,[1] K. C. PARKES,[2] G. B. REYNARD,[3] A. KIRKCONNELL,[1] AND R. SUTTON[4]

ABSTRACT.—The systematics of the genus *Spindalis* of the Greater Antilles and Cozumel Island, off Yucatan, are herein analyzed. Meristic data, coloration, and weight of the eight described taxa are compared. A table with extremes and means of all measurements is provided. Vocalizations of most of the principal taxa are compared. Final analysis of these comparisons suggests that rather than representing a single polytypic species, this complex is a superspecies with four allospecies: *zena, portoricensis, dominicensis*, and *nigricephala*. Therefore the Jamaican population becomes an endemic species, *Spindalis nigricephala*, as does the Puerto Rican *S. portoricensis*. Hispaniola and Gonave Island are inhabited by *S. dominicensis*. The fourth allospecies, *S. zena*, is a polytypic species represented by five endemic subspecies: *S. z. zena* in some islands of the Northern and Central Bahamas; *S. z. townsendi* confined to Grand Bahama, the Abacos, and Green Turtle Cay; *S. z. pretrei* in Cuban territory; *S. z. salvini* confined to the island of Grand Cayman; and *S. z. benedicti* confined to Cozumel Island, east of the Yucatan Peninsula, Mexico. A zoogeographic comparison with other endemic West Indian genera is presented. *Received 11 June 1996, accepted 1 May 1997.*

RESUMEN.—El presente trabajo analiza la situatión sistemática de los ocho táxones del género *Spindalis* en las Antillas y en la isla de Cozumel, tomando en consideración las diferencias morfológicas (medidas, patrón, peso, diseño y coloración) en ambos sexos, resumidas en una tabla con sus medias y extremos. Una comparación de sus vocalizaciones es también expuesta, con sonogramas de algunos de los principales taxónes. El resultado de estas comparaciones sugiere que no estamos en presencia de una espccie politípica, sino de una superespecie con cuatro aloespecies bien diferentes: *zena, portoricensis, dominicensis* y *nigricephala*, por lo tanto la población de Jamaica está representada por una especie endémica, *Spindalis nigricephala*, al igual que Puerto Rico con *Spindalis portoricensis* y *Spindalis dominicensis* en Santo Domingo, incluyendo la Isla de Gonave. La cuarta alocs-

[1] Museo Nacional de Historia Natural, La Habana, Cuba.
[2] Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213.
[3] 105 Midway Street, Riverton, New Jersey 08077.
[4] Marshall's Pen, P.O. Box 58, Mandeville, Jamaica.

pecie, *Spindalis zena*, es una especie politípica, representado por cinco subespecies endémicas: *Spindalis zena zena*, presente en algunas islas del norte y centro de las Bahamas; *S. z. townsendi*, confinada a las islas Abaco y Grand Bahama y a Green Turtle Cay, del norte de las Bahamas; *S. z. pretrei*, representada en el territorio cubano; *S. z. salvini*, confinada a la Isla de Gran Caymán, y *S. z. benedicti*, confinada a la isla de Cozumel, al este de la península de Yucatán. Se especula sobre el presunto aislamiento geográfico de estas poblaciones, así como se correlaciona el género *Spindalis* con otros géneros representados en las Antillas que pueden constituir presuntas de formas vicariantes.

The genus *Spindalis* Jardine and Selby, 1837, comprising the Stripe-headed Tanagers, is endemic to the Greater Antilles; a peripheral population on Cozumel Island, east of the Yucatan Peninsula, is part of the West Indian element in that island's fauna (Bond 1936). The relationship of *Spindalis* to mainland genera of tanagers is, to say the least, unclear. Three modern lists (Hellmayr 1936, Storer 1970, Sibley and Monroe 1991) agree in placing *Spindalis* between *Thraupis* and *Ramphocelus*. It is doubtful that this sequence is based on any critical study, as it has been repeated consistently since Sclater's "Synopsis Avium Tanagrinarum" (1856–1857), in which the classification was based in large part on differences in bill shape. Storer (1970, followed by Isler and Isler 1987) suggested a relationship between *Spindalis* and *Thraupis bonariensis* of southern South America. The lack of blue (conspicuous in all *Thraupis* except *T. palmarum*) in the plumage of *Spindalis* and the remoteness of the range of *T. bonariensis* from that of *Spindalis* makes such a relationship unlikely. In many ways, the plumage pattern of the Bananaquit (*Coereba*) resembles that of *Spindalis* more than does that of *T. bonariensis*, although this is not suggested as an indication of close relationship. It can be safely stated that the true relationship of *Spindalis* to mainland tanagers has yet to be determined.

Bryant (1866) proposed splitting the genus *Spindalis*, introducing the generic name *Spizampelis* for the group of taxa comprising the forms *pretrei, zena*, and *nigricephala*. This proposal has never been accepted, and Ridgway (1902) placed *Spizampelis* in the synonymy of *Spindalis*.

The Stripe-headed Tanager, according to Hellmayr (1936), Bond (1956), and the 6th edition of the American Ornithologists' Union Checklist (1983), consists of a single polytypic species, *Spindalis zena*, with eight recognized subspecies. These taxa are: *S. z. townsendi* and *S. z. zena* in the Bahaman archipelago; *S. z. pretrei* in the Cuban archipelago, *S. z. salvini* on Grand Cayman Island; *S. z. dominicensis* in Hispaniola and Gonave Island; *S. z. portoricensis* in Puerto Rico, *S. z. nigricephala* in Jamaica, and *S. z. benedicti* on Cozumel Island, Mexico. All of these forms except *townsendi* were originally described as species. In addition

to these eight forms, five other names have been proposed: *stejnegeri* Cory (1891) for the island of Eleuthera in the Bahamas; *pinus* Bangs and Zappey (1905) for the Isle of Pines (now the Isle of Youth), Cuba; *exsul* Salvin (1885) for Cozumel Island; *bilineatus* Jardine and Selby (1837) for Jamaica; and *multicolor* Vieillot (1822) for Hispaniola and the Bahamas. The names *exsul* and *bilineatus* are objective junior synonyms of *benedicti* and *nigricephala*, respectively. According to Hellmayr (1936), *stejnegeri* "seems to be an individual mutant without geographical significance," and he synonymized this name with *zena*. As for *pinus*, Todd (1917) pointed out that the alleged color characters differentiating it from *pretrei* were based on seasonal differences, and size overlapped too much to warrant recognition of *pinus*.

Allocation of the name *multicolor* Vieillot (1822) is more complicated. In Vieillot's description he clearly confused, under one taxon, the birds from Hispaniola and the Bahamas, as he mentioned having seen both (Bryant, 1867). In his description of the male, the characters agree perfectly with the Bahaman bird (already described by Linnaeus as *zena*), as it is the only form in the entire complex with a black back. Hellmayr (1936) believed that the description of the female of *multicolor* was based on the Hispaniolan bird, and therefore listed "*multicolor*, part" in the synonymy of *dominicensis* Bryant. However, Vieillot's description of the female did not mention streaked underparts, which are typical of the Hispaniolan population. The description of the female matches those of the Bahamas, so that Hellmayr's allocation of Vieillot's description as divided between the synonomies of *zena* and *dominicensis* was erroneous, and *multicolor* Vieillot is a synonym of *zena*.

Some authors, such as Ridgway (1902) and Hellmayr (1936) have cited the original description of *dominicensis* as "Bryant 1866." This paper was part of the proceedings of the meeting of the Boston Society of Natural History in December 1866, but was not actually *published* until May 1867, so the latter date is the correct citation, as given by Wetmore and Swales (1931) and Bond (1956).

The number of species to be recognized in the genus *Spindalis* has been much debated. James Bond changed his mind several times on this question. In his first book (1936) on West Indian birds, he listed six species, with only *zena* as polytypic (i.e., including *townsendi*); he did not mention *benedicti* of Cozumel Island, which was extralimital. In 1945, he wrote "Although the forms of *Spindalis* are geographically representative of one another, it obscures their affinities to regard them all as conspecific. Bahaman and Cayman Island birds and the one extralimital race from Cozumel were probably derived from Cuba." In accordance with the latter statement, he included *townsendi, pretrei, salvini*, and *be-*

nedicti in *zena*, recognizing *dominicensis, portoricensis,* and *nigricephala* as full species, thus going from six to four species in the West Indies. In his 1956 check-list Bond again admitted only a single species, but wrote in a footnote "Perhaps a more satisfactory taxonomic treatment of the genus *Spindalis* would be the recognition of three species based primarily on the coloration of females (i.e., *S. zena, S. dominicensis,* and *S. nigricephala*)." Nevertheless he continued to admit only a single species as late as the fifth edition (1985) of his field guide. Other recent authors of regional works who have listed their resident form as a race of *Spindalis zena* include Garrido and García Montaña (1975), Dod (1978, 1981), Raffaele (1983), Bradley (1985), and Downer and Sutton (1990). In check-lists, Storer (1970) and the A.O.U. (1983) recognized only one species of *Spindalis*.

Steadman et al. (1980) compiled a table of weights of West Indian birds they had obtained in the field. They quoted Bond's 1956 statement suggesting the possibility of dividing *Spindalis* into three species based mainly on coloration of females, and went on to say "Our data on weights supports this treatment." This was based on their finding that Jamaican *Spindalis* weighed approximately twice as much as those from the Bahamas and Hispaniola. In their table they used the names *Spindalis z. zena, S. zena townsendi, S. portoricensis dominicensis,* and *S. nigricephala*. Differences in body weight alone should not be sufficient for species status, as there are no doubt several polytypic species in which the largest subspecies weighs twice as much as the smallest (the Song Sparrow, *Melospiza melodia,* comes to mind). Moreover, Steadman et al. did not have weights for *benedicti,* although these have been published by Paynter (1955). The weights given by Paynter exactly match those on labels of specimens in the Carnegie Museum of Natural History. At 26–36 gm, they fall midway between those of *nigricephala* and those of the smaller taxa, thus making the large size of *nigricephala* less striking.

If three species are to be recognized, there is disagreement as to their names. The A.O.U. (1983), although treating *Spindalis* as monotypic, repeated Bond's suggestion that the three should be *zena, dominicensis,* and *nigricephala,* but as indicated above, Steadman et al., used the species names *zena, portoricensis,* and *nigricephala*. They were correct insofar as nomenclature is concerned, as when Hispaniolan and Puerto Rican populations are combined into a single species, the name *portoricensis* Bryant, 1866, has priority over *dominicensis* Bryant, 1867. In addition to the AOU Checklist (1983), works that erroneously use the junior name *dominicensis* for the combined Hispaniolan and Puerto Rican populations include Bond (1956), Sibley and Monroe (1990), and its offshoot, Monroe

and Sibley (1993). The latter two works admit only a single species of *Spindalis*, but list "groups" recognized as species by some authors.

Amadon and Short (1976) introduced the term "megasubspecies" for "well-marked forms approaching the level of species, but nonetheless judged to be conspecific." One of their examples was the genus *Spindalis*, which they divided into five megasubspecies. One of these, *zena*, would consist of what they called "the minor subspecies *townsendi* and *zena* together." Unfortunately they used the erroneous name *multicolor* for the Hispaniolan "megasubspecies," and overlooked the Cozumel and Grand Cayman populations, *benedicti* and *salvini*. Their proposal has had little or no support.

Spindalis is a non-migratory West Indian genus, with the only extralimital race, *benedicti* of Cozumel Island, being an obvious derivative from one of the West Indian populations. Although larger than any of the members of the *zena* complex (Cuba, Bahamas, Grand Cayman), the resemblances in color of both males and females to members of that group strongly suggest that the affinities of the Cozumel Island population are with the *zena* complex. The resemblances of *benedicti* are a mosaic of the other members of that complex; nearest *townsendi* in back and upper breast color of males, nearest *zena* in nuchal collar and rump color of males, nearest *salvini* in intensity of yellow on throat and lower breast of males, and nearest *pretrei* in tail pattern of females.

The biological species concept is difficult to apply when dealing with allopatric populations, because there is no direct evidence for presence or absence of reproductive isolation (Mayr and Short 1970). Radiations of closely allied forms at uncertain levels of speciation have occurred in several West Indian groups, in amphibians and reptiles as well as in birds. Parkes (1991) has discussed the difficulties of assessing the taxonomic status of replacing forms in an archipelago, with special emphasis on the Philippines, but mentioning the *Spindalis zena* and *Tyrannus* (*Tolmarchus*) *caudifasciatus* groups as examples of problem groups in the West Indies. Vocalizations play an important role in the discrimination of mainland species, but differences in vocalizations among allopatric insular forms are not necessarily indicative of species status in the absence of other differences. However, when such differences are combined with morphological, ecological, or ethological differences, vocal evidence can be given great weight; such is the case in *Spindalis*.

The objective of the present study is to reexamine the members of the genus *Spindalis* in the light of the various opinions as to the number of species to be recognized.

MATERIALS AND METHODS

Garrido and Kirkconnell examined 369 skins (253 males and 116 females) of *Spindalis*, housed in the following institutions: American Museum of Natural History, New York

TABLE 1

MEASUREMENTS (IN MM) OF *SPINDALIS* SP.[a]

	Wing (flat) (except *nigricephala* = chord)			Tail		
	N	Range	Mean ± SD	N	Range	Mean ± SD
MALES						
S. z. pretrei	(42)	69–80	75.1 ± 2.493	(41)	51–61	55.6 ± 2.106
S. z. salvini	(18)	80.5–87	83.4 ± 1.739	(19)	56–65.5	62.4 ± 2.235
S. z. benedicti	(12)	79.5–86	82.0 ± 2.089	(11)	61–70	64.0 ± 2.485
S. z. townsendi	(26)	75–82	78.6 ± 2.232	(26)	54–65	59.7 ± 2.813
S. z. zena	(78)	72–84	77.8 ± 2.479	(76)	52–66	58.8 ± 2.718
S. portoricensis	(26)	82–88.5	85.2 ± 1.891	(26)	59–68	63.6 ± 2.244
S. dominicensis	(24)	80.5–93	85.8 ± 4.316	(24)	61–75	66.7 ± 3.863
S. nigricephala	(16)	94–103	99.6 ± 2.410	(16)	70–80	74.8 ± 3.194
FEMALES						
S. z. pretrei	(18)	68–75.5	72.0 ± 2.233	(18)	49.5–57	52.9 ± 2.002
S. z. salvini	(4)	78.5–83	80.4 ± 2.057	(4)	58–63.5	59.5 ± 2.677
S. z. benedicti	(9)	76.5–80.5	78.6 ± 1.424	(9)	55.5–61	59.1 ± 1.828
S. z. townsendi	(13)	72–76.5	74.3 ± 1.640	(13)	53–58	55.3 ± 1.186
S. z. zena	(27)	69.5–78	73.8 ± 2.206	(30)	52–58.9	54.9 ± 2.119
S. portoricensis	(12)	80–85.5	82.6 ± 1.649	(11)	56–65.5	60.6 ± 2.290
S. dominicensis	(21)	77–88	81.7 ± 3.164	(20)	55–66	61.6 ± 3.302
S. nigricephala	(11)	90–98.5	95.4 ± 2.548	(12)	67–76	72.3 ± 2.879

[a] (N).

(AMNH); Royal Ontario Museum, Toronto; Institute of Jamaica, Kingston; Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba; Universidad de la Habana, Cuba; and Museo Nacional de Historia Natural, Cuba. Data from these specimens were supplemented by 65 males and 33 females examined by Parkes in the Carnegie Museum of Natural History (CM); the series of *portoricensis* and *townsendi* were substantially larger than those available to the other authors. In order to study individual variation in *townsendi*, Parkes borrowed series from the Field Museum of Natural History (FMNH) and the Museum of Natural Science, Louisiana State University (LSU). Sutton obtained his data from banded birds. Table 1 presents available weights (in g) and the conventional measurements (in millimeters) of the wing (flattened), tail, tarsus, and exposed culmen. Egg measurements, also in millimeters, are taken from the literature. Vocalizations were recorded in Puerto Rico, the Dominican Republic, Cuba, Jamaica, and Grand Cayman by G. B. Reynard; in Puerto Rico by José Colón; in Jamaica and Grand Cayman by Robert Sutton; in the Bahamas by Paul Dean and P. P. Kellogg (Library of Natural Sounds [LNS], Cornell University collection); in the Dominican Republic by T. Parker III (LNS); and on Cozumel Island by R. B. Waide (also LNS). Tape recordings were made using several models of Nagra, Uher reel-to-reel types, and a Sony TM 5000 cassette recorder, usually with microphones in 61 or 91 cm parabolic reflectors. Sonograms were made using Kay Elemetrics equipment. Published recordings include those made by Reynard and his colleagues in Puerto Rico, Hispaniola, and Cuba (Reynard, 1969, 1981; Reynard and Garrido, 1988). Weights of birds were taken in Cuba by R. Piechoki, K. Uhlenhaut, O. Garrido, and A. Kirkconnell; in Puerto

TABLE 1
EXTENDED

Culmen			Tarsus		
N	Range	Mean ± SD	N	Range	Mean ± SD
(37)	10.1–13.1	11.0 ± 0.727	(38)	17.5–23	20.1 ± 1.380
(19)	10.1–12.5	10.7 ± 0.561	(17)	19.5–22.6	21.3 ± 0.946
(12)	12.8–14.7	13.8 ± 0.744	(12)	19.5–23	21.1 ± 1.296
(25)	10.4–12.9	11.7 ± 0.695	(26)	18.8–23.5	20.7 ± 1.234
(78)	9.6–13.8	11.2 ± 0.709	(76)	18.5–23.5	20.7 ± 1.049
(25)	10.4–13	11.7 ± 0.605	(25)	19.5–23.5	20.7 ± 1.037
(24)	8.7–10.8	9.7 ± 0.575	(24)	18.5–23	20.7 ± 1.070
(17)	10.4–13.5	12.4 ± 0.905	(13)	21–24.5	22.2 ± 1.140
(18)	9.7–12.2	11.0 ± 0.727	(18)	17.4–21.2	19.7 ± 1.167
(5)	10.3–11.5	10.6 ± 0.546	(5)	20.5–23.8	21.4 ± 1.374
(8)	10.7–13.7	12.2 ± 1.370	(9)	20.5–22.8	21.2 ± 0.918
(13)	9.7–11.2	10.5 ± 0.514	(12)	18.2–21.7	20.5 ± 1.159
(30)	9.1–11.4	10.4 ± 0.500	(28)	18.5–23	20.9 ± 1.183
(12)	10.7–12.3	11.5 ± 0.504	(12)	19.5–23	21.1 ± 1.135
(21)	7.6–10.1	8.9 ± 0.697	(20)	19–23.5	21.4 ± 1.551
(12)	10.1–15.1	12.4 ± 1.213	(10)	21.5–23.2	22.4 ± 0.549

Rico by Olson and Angle (1977); in the Cayman Islands by Olson et al. (1981); in the Bahamas, Hispaniola, and Jamaica by Steadman et al. (1980); in Jamaica by Robert and Ann Sutton; and in Cozumel Island by Paynter (1955) and Parkes (Table 2).

In coming to our conclusions, we have also consulted the data published by Ridgway (1902) and remarks on systematics of *Spindalis* by the several other authors cited in this paper.

Comparisons

Although Ridgway (1902), Hellmayr (1936), and Bond (1936) gave diagnostic characters and partial descriptions of all forms of *Spindalis*, they did not make full comparisons among all of them. We make such paired comparisons here. Suggestions for dividing *Spindalis* into several species have emphasized characters of females, but males also exhibit striking differences in color and pattern. For mensural characters, see Table 1.

I. The *zena* complex. This group has the following characters in common: females essentially olive green with no bright colors, unstreaked ventrally; males with nuchal collar and rump patch of various mixtures of chestnut and yellow; a chestnut band (brownish orange in some individuals of *pretrei*) across upper breast, separating the yellow of the throat

TABLE 2
WEIGHTS (IN GM) OF *SPINDALIS* SP.*

	N	Range	Mean	SD
MALES				
S. z. pretrei	19	18.5–25.5	22.0	1.62
S. z. salvini	16	20.5–31.0	23.1	1.54
S. z. benedicti	9	26.8–35.6	30.8	3.20
S. z. zena	11	19.2–23.2	21.1	1.36
S. portoricensis	109	22.5–37.0	30.8	2.82
S. nigricephala	111	38.0–64.8	43.0	0.20
S. nigricephala (Robbins)	29	38.0–54.1	44.7	3.53
FEMALES				
S. z. pretrei	12	18.0–25.0	22.4	2.07
S. z. salvini	8	24.0–28.5	25.5	0.31
S. z. benedicti	6	26.5–32.8	30.0	2.37
S. z. zena	7	17.0–25.5	21.7	2.58
S. portoricensis	42	28.0–41.1	33.5	3.30
S. nigricephala	48	45.2–53.7	47.2	**
S. nigricephala (Robbins)	6	38.0–50.7	44.0	4.38

* Adequate weight samples were not available for *S. z. townsendi* and *S. dominicensis*.
** SD not computed.

and that of the lower breast; tail black with varying amounts of white but always with outer and central rectrices edged in white.

1. *Pretrei* versus *salvini*: In males of *salvini* the color of the chest averages richer and is more extensive anteriorly, extending farther forward than in *pretrei*, reducing the size of the yellow patch on the lower throat. The white of the chin extends posteriorly between the black malar stripe and the yellow throat patch, further restricting the latter. In *pretrei* the white superciliary line is continuous, whereas in *salvini* it is broken by black or black-tipped feathers above the eye. Dorsally, *salvini* is slightly darker green on the mantle. The nuchal band is strongly bicolored—chestnut anteriorly and narrowly yellow posteriorly. In *pretrei* the division between chestnut and yellow is less clearly defined. The rump of *salvini* is chestnut, the feathers narrowly bordered with yellow; the anterior margin of the chestnut area is narrowly greenish yellow. The rump of *pretrei* is more orange, with a less distinct anterior border of yellow. Females are very similar; *pretrei* is slightly greener, less gray dorsally than *salvini*. The whitish malar stripe is more conspicuous and more clearly defined along its lower margin in *pretrei*. The white patch on the outermost rectrix

is more extensive anteriorly in *pretrei*. *Salvini* averages slightly larger than *pretrei* in all dimensions.

2. *Pretrei* versus *benedicti*: In males of *benedicti* the color richness seen in *salvini* goes even farther. The breast is much darker chestnut, becoming blacker anteriorly and blending with the posterior end of the black malar stripe. The yellow throat patch is restricted by the black malar stripe. The rump and nuchal band of *benedicti* are dark chestnut, with narrow yellow tips to some of the feathers. The green of the back is much darker with a brownish cast. In females, *benedicti* is very slightly darker green dorsally and on the breast than *pretrei*. The whitish malar stripe is obsolete, the throat being barely paler laterally than centrally. The amount of whitish in the inner webs of the outer two pairs of rectrices is variable but usually more than in *salvini* and less than in *pretrei*. *Benedicti* is the largest of the forms in the *zena* group, being somewhat larger than *salvini* and decidedly larger than the other forms. This is particularly conspicuous in the bill.

3. *Benedicti* versus *townsendi*: Males of these two forms are quite similar in color. The yellow of the underparts of *townsendi* is richer with a slight orange tinge. The chestnut on the breast of *townsendi* is almost as dark as in *benedicti*, but slightly less extensive. The green of the mantle of many *townsendi* is nearly identical with that of *benedicti*, although many *townsendi* have the dorsum washed with blackish, an approach to *zena*. The nuchal band and rump of *townsendi* are conspicuously bordered with yellow posteriorly and anteriorly, respectively; in *benedicti*, the margin of the chestnut is barely yellower than the mantle. Females are indistinguishable in color, separable only by size.

4. *Zena* versus *townsendi*: *Zena* is the only member of its group in which the mantle of males is black rather than greenish. This increase in melanin is also manifested in the black malar stripe, which is much wider than in any other form (except in some Bahaman specimens), restricting the yellow throat patch to a more linear shape and the chestnut of the breast to a central spot. The nape and rump are strongly bicolored, as in *townsendi*, but the chestnut averages darker and the yellow border narrower and more sharply defined.

Individual variation in *zena* is most noticeable in the underparts. The breast varies from entirely chestnut (the posterior feathers yellow-edged) to the chestnut being confined to a narrow transverse area just below the chestnut extension of the yellow throat patch. In many individuals, the yellow throat is mixed with chestnut; this is not necessarily correlated with the amount of chestnut on the breast. Neither of these characters is correlated with age; both extremes can be found in both age classes. The sides and flanks are olive-gray, as in the other subspecies of the *zena*

group, although perhaps slightly darker. However, this area is sometimes faintly streaked with black and occasionally heavily streaked (CM 30659, 1st year bird). Although the male of this subspecies is always characterized as having a black back, the dorsal feathers are occasionally inconspicuously and narrowly edged with orange-brown, being seen only in the hand and in good light (1 of a CM series of 6 from Blue Hills, Nassau, 30 December–15 January 1908–9).

Individual variation in males of *townsendi* is of particular interest, as it appears to exceed that found in any other subspecies. For this study, Parkes assembled an unprecedented series of 68 males from FMNH and LSU to supplement the 14 in CM. Of these 82, 45 were from Great Abaco (type locality of *townsendi*) and 37 from Grand Bahama.

The chestnut breast band is narrow and less variable in extent than in *zena*, from a slight extension of the chestnut throat area (FMNH 27703) to a relatively broad lateral extension much mixed with yellow (FMNH 27284), but never as extensive posteriorly as in extremes of *zena*. The yellow of the throat is seldom as intensely orange as in *zena*, although more-or-less streaked with chestnut in 24% of Abaco specimens examined. The width of the malar stripe and consequent restriction of the yellow throat area is variable, matching *zena* in this respect in some individuals.

The most variable area is the back. It ranges from unmarked greenish orange to black with dull orange feather edgings. This is not correlated with age. Those with the black extreme constitute 14 of 45 (31%) of the Abaco specimens. This variability was recognized by Ridgway (1887), who described *townsendi* from five males and three females from Abaco.

Males from Grand Bahama do not differ from Abaco birds except in back color. The black extreme is much less common on Grand Bahama. In the series examined, only three of 37 specimens (8%) matched the black individuals in the Abaco series. This difference may well be explained by a limited gene flow from the black-backed *zena*. Abaco is closer than Grand Bahama to New Providence, the nearest island inhabited by *zena* (and in fact its type locality). That *Spindalis* can move from island to island is demonstrated by Buden (1987), who stated that *zena* invaded Providenciales Island in the Caicos Islands (the nearest island to the southern Bahamas) in the 1970s.

Females of the two Bahaman forms are much more similar than the males. The ventral color is identical. Some individual females of *townsendi* may have almost imperceptible blackish shaft-streaks on the mantle; these are better developed in *zena*, in which the crown may also be faintly spotted with blackish.

II. *Nigricephala*. This is the most distinctive *Spindalis*, both in color and in size. It is the largest, weighing twice as much as the smallest form,

zena (Table 1). Males differ from all other forms in lacking yellow on the chin, which is white. In adult males, the broad black malar stripes merge across the upper breast; in first-year males the connection is narrower, the black being parted by an extension of the orange of the breast. There is no chestnut on the breast. Below the black, the breast is rich, glossy orange, and the yellow of the posterior underparts, unlike the members of the *zena* complex, extends all the way to the abdomen; only the under tail coverts and (in some) a few adjacent abdominal feathers are white. The back is purer green than in any of the *zena* complex, and there is, at best, only a faint trace of a nuchal band (see photograph on p. 122 of Downer and Sutton 1990). The rump varies from being merely a bit paler than the mantle to dull orange. The bend of the wing is black, lacking any trace of the chestnut patch found (in varying degrees of size and depth of color) in all other males of *Spindalis*. The narrow outer endgings of the remiges are yellowish in first-year birds, white in older males. White on the tail is confined to R6, the outermost rectrix (with an occasional trace at the tip of R5), and is much less extensive than in the *zena* complex.

The brightly colored females of *nigricephala* are unique in the genus *Spindalis*. The underparts, from the breast to the lower abdomen, are yellow, tinged with orange on the upper breast. The under tail coverts and a variable amount of the lowermost abdomen are grayish white. The throat is light neutral gray, contrasting sharply with the orange-yellow (and often a central bright orange area) of the upper breast. The chin, malar stripe and superciliary are indistinctly paler than the throat. The crown and nape are darker gray, washed with greenish in fresh plumage. With wear, the green overlay is lost, and, in some individuals, whitish shaft-streaks are revealed on the crown and ear coverts. The mantle is much greener than in any member of the *zena* complex, and only slightly darker than in males of *nigricephala*; as in the former, the rumps of females are brighter and yellower. White in the rectrices is confined to an edging on the terminal quarter of the inner web of R6 and, sometimes, a trace in the same area of R5. The tail and wings are blacker than in the *zena* complex, and the edgings of wing feathers whiter, thus almost as conspicuous as in males.

III. *Dominicensis* and *portoricensis*. The two remaining forms have one distinctive character in common; females and juvenile males have streaked underparts. Adult males, however, are quite different from one another. Comparisons with other forms are as follows.

1. *Dominicensis* versus the *zena* complex: In males the color and pattern of the underparts are quite similar to those of *salvini*, except that the yellow of the abdomen of *dominicensis* is richer and extends farther pos-

teriorly. Dorsally, however, *dominicensis* is unique. The mantle feathers are black at the base and tipped with yellow, giving a dark yellow-green effect. The nuchal collar is broader than in any other form and is brilliant yellow, with an orange tinge anteriorly. The rump color is much as in *salvini*, except that the yellow of the anterior margin is deeper and contrasts more with the mantle. The chestnut patch at the bend of the wing is the most extensive in the genus, including all but the tips (which are black) of the lesser coverts. As mentioned above, females differ from those of the *zena* complex in having narrow blackish streaks on the underparts; the base color is much as in *townsendi*. Dorsally, females of *dominicensis* are greener than any in the *zena* complex, and the rump is distinctly yellowish, contrasting sharply with the mantle. Males in juvenal plumage are heavily streaked ventrally with blackish streaks on a white background. Unlike adult females, they are also streaked dorsally, although the blackish streaks are inconspicuous against the dark green background. The rump is like that of adult females but with a slight chestnut tinge.

2. *Portoricensis* versus the *zena* complex: Definitively plumaged males differ from all of the *zena* group in several ways. At least in 19 CM specimens from west–central and eastern Puerto Rico (Utuado, Adjuntas, Guayama, Fajardo) there is no trace of chestnut on the breast; instead, there is a small patch of bright, glossy orange feathers, similar to those of *nigricephala*, just posterior to the yellow throat (as shown on the color plate). F. Vilella (in litt.) states that he has seen males in western Puerto Rico with some chestnut on the breast, so there is at least the possibility of geographic variation in this character within Puerto Rico. The throat and the white chin are conspicuously spotted with black (some other races, such as *benedicti* and *townsendi*, may occasionally have a few tiny black spots on the throat). The yellow of the lower breast is greener than in any of the *zena* group. Even in definitively plumaged males, there are vague gray streaks on the whitish flanks. The green of the mantle is nearest that of *salvini*, but slightly darker. There is a narrow, bright orange nuchal collar, faintly tinged with chestnut at the anterior edge. Unlike all of the *zena* group, there is no contrasting rump patch; the rump feathers are merely a slightly brighter yellow-green than the mantle. First-year males are highly variable and differ from older males in being streaked with dark gray on the sides and flanks and even to some extent in the yellow of the breast. The yellow is less extensive posteriorly than in the older birds and is variable in extent. There is just a hint of the orange spot at the posterior border of the yellow throat patch. Dorsally, the two age classes of males are much alike, but in at least some of the younger birds, the mantle feathers have inconspicuous narrow black shaft streaks.

The rectrices of male *portoricensis* are unique. Rather than being black with a large white patch, as in all other *Spindalis*, they are dark olive brown, edged externally (when fresh) with yellowish green, like those of the female. White is confined to a narrow line on the outer margin of the inner web of the two outermost rectrices.

Females of *portoricensis*, like those of *dominicensis*, differ from the *zena* group in being streaked ventrally. As in males, there appear to be two age classes subsequent to the juvenal plumage. In what we take to be the younger birds, the streaks are somewhat blurred; the background color, although not pure white, is paler than in any member of the *zena* group. The mantle color is dark, as in *benedicti*, but greener and less gray, and, unlike *benedicti*, the rump is brighter green than the mantle (but not as much so as in *dominicensis*). There are a sharply contrasting white malar stripe and a narrow superciliary stripe similar in its development to that of *pretrei* but whiter. In older females the mantle is slightly brighter green, and there is a narrow greenish-yellow nuchal collar. The streaking of the underparts is more sharply defined than in the younger birds, and the breast is saturated with bright greenish yellow, tending toward orange anteriorly and continuing as a faint yellow wash back to the abdomen. The white malar stripe is equally prominent, but the superciliary stripe is obsolescent.

In summary, males (collectively) of the *zena* group (*pretrei, salvini, zena, townsendi, benedicti*) are characterized by having varying amounts of chestnut on the breast, rump, and nuchal collar (listed above in increasing sequence of chestnut pigmentation). Males of *dominicensis* have the chestnut of breast and rump developed about as in *salvini* but lack chestnut in the nuchal collar which is broad and brilliant orange-yellow. The mantle differs from all of the *zena* group in consisting of black feathers with yellow tips. Males of *portoricensis* lack chestnut entirely (except possibly on the breast in western Puerto Rico), have black-spotted throats, streaked flanks (especially in first-year birds), no contrasting rump-patch, and female-like rectrices. Males of *nigricephala*, in addition to their great size, are unique in lacking a nuchal collar and in having the throat white rather than yellow. They also lack a rump patch and any chestnut in the plumage.

The females of all of the *zena* group are slightly varying shades of greenish gray, scarcely if at all paler on the rump, and with no markings on body plumage except a tendency for whitish malar and superciliary stripes. Females and juveniles of *dominicensis* and *portoricensis* are unique in having streaked underparts; those of *dominicensis* differ in having the rump conspicuously brighter than the mantle. Females of *nigri-*

cephala, in addition to their great size, are unique in having brilliant yellowish underparts, strongly contrasting with their neutral gray heads.

Vocalizations

This group of tanagers is characterized by the high-pitched notes they emit, some at or above 8 khz. Songs can be difficult to detect because of their ventriloquial quality and because males may sing from the highest treetops. Females characteristically sing their "whisper songs" when hidden in dense thickets; one we recorded was less than 0.5 m above the ground. In the effort to characterize the songs assembled for this study, we lack the advantage of having any published full life history studies of any of the populations of *Spindalis* but hope our information will spur others to continue studies of this interesting genus!

Sound tapes described are from unpublished material in the Cornell Library of Natural Sounds, our new recordings, and from three publications covering Puerto Rico, Hispaniola, and Cuba (Reynard 1969, 1981; Reynard and Garrido 1988), respectively.

Prior to those published recordings, several authors had written subjective descriptions of *Spindalis* vocalizations. Bond (1936:369) generalized by writing: "with the exception of the Cuban and Bahaman species, which possess a prolonged but remarkably weak song, I have never heard them emit more than a shrill, drawn out *seep*." Other published descriptions will be entered in the island by island discussion along with the analyses of vocalizations presented here.

Puerto Rico.—Wetmore (1927) wrote of the Puerto Rican birds: "The call-note is a faint "*tseet*", and males give a low chattering note. I heard no song from them, but Danforth has recorded a weak though spritely effort heard very rarely." On the other hand, according to Raffaele (1983), the Puerto Rican bird does sing: "Its thin, but distinctive song can be heard commonly during the breeding season *zeé-it-zeé-tittit-zeé*. The *zeé* syllable often seems like an inhaling sound. This basic call has many variations. A thin trill like the beating of a tiny hammer is rarely heard as is a short twittering call. The call note is a soft '*teweep*.' The distinctive principal call in our recordings (Fig. 1A) is a continuing series of high-pitched, thin, sibilant notes, given in a rhythmic pattern, much like that described by Raffaele, which we paraphrased as "*seet see seee seet see seee seet see seee*," given repeatedly in groups of three of the 3-note phrases, two of which are shown in Fig. 1A. The short songs were separated by ca. 4 sec pauses.

Among other vocalizations recorded are a fast "*twitter*" (Fig. 1B) and a short "*chi chi chi*," descending in pitch (Fig. 1C). Three intense, very high-pitched, squeaky "lisps," resembling a "*tseee er*" phrase (Fig.

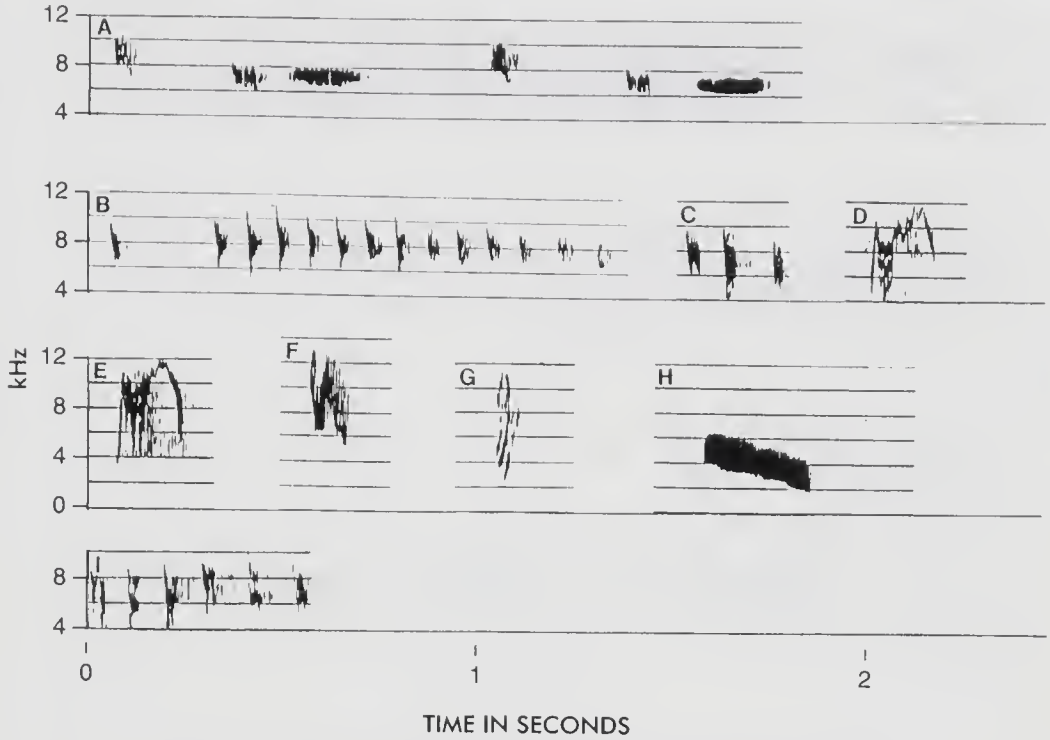

FIG. 1. Vocalizations of *Spindalis portoricensis* (see text).

1D,E,F) are probably aggression calls. An apparent "contact call," during feeding sessions (Fig. 1G) is a "*queet*" sound, rapidly ascending in pitch. The descending whistle (Fig. 1H), of undetermined context, is lower in frequency than most other calls. A short, rapid chatter is a "fly-off" vocalization; it was accompanied by "clicks" from wing fluttering, which resulted in some of the vertical, faint lines in the sonogram (Fig. 1I).

Hispaniola.—Wetmore and Swales (1931) stated of Hispaniolan *Spindalis*: "They are very silent and seldom call, their note then being low and faint. Wetmore heard one utter a weak, sibilant song that may be written *tsee see see see*, in so low a tone that it was heard with difficulty, which agrees with Verrill's notes that the song is feeble and insect-like" (Verrill and Verrill 1909).

The weak song referred to above is not in our collection of tapes, but consists of "seep" notes given more rapidly than those shown here (Fig. 2A), which were recorded during an introductory period before initiation of a song series. This is considered a territorial song.

The "twitter" (Fig. 2B) and the low-pitched double "churrs" (Fig. 2D) are believed to be conflict-related calls. A "whisper song" from a female (Fig. 2C) was typically weak, lacked evident rhythm, with ever-changing syllables, in a more or less recitative or conversational pattern. A heavy background chorus obscured the tanager voice in the original recording, so this is a tracing from the original sonogram.

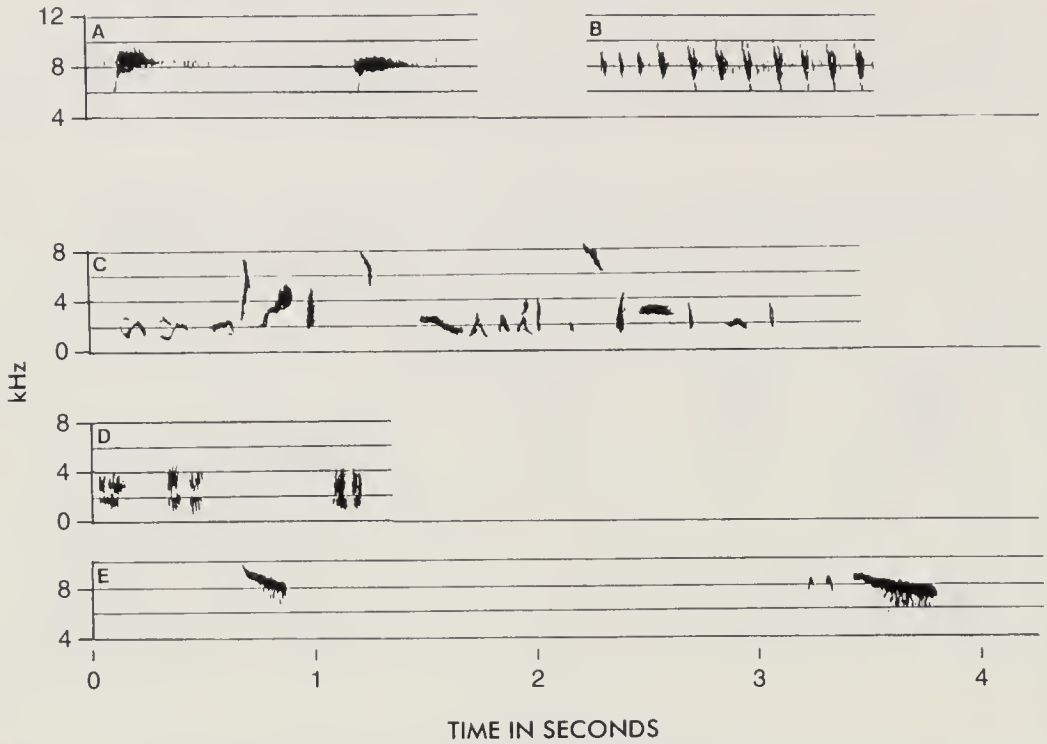

FIG. 2. Vocalizations of *Spindalis dominicensis* (see text).

The Bahamas.—Of the two forms of *Spindalis* found in the Bahamas, we know of neither a description nor a recording of the vocalizations of *townsendi* of the northern Bahamas.

Brudenell-Bruce (1975) wrote of *zena* on New Providence: "the song at the beginning of the season is a weak twittering, but it becomes more vigorous and varied as the summer progresses. Though uninteresting from a distance, it is surprisingly sweet and melodious from close to. Usually sings from a high perch, often the very top of a tree: also in flight, when a male flies from the topmost point of a pine or casuarina, circles round with slowly beating wings, in full song, and then dives down to the same or another perch. . .There is a lyrical subsong, so soft as to be almost inaudible. The call-note is a loud 'seeip'. Small flocks keep up a soft 'tit-tit-tit' or 'si-si-sit', often hard to locate."

The description by Brudenell-Bruce is the only report we have seen of a flight song in *Spindalis*, although some use fast calls in flying off. We have no recording of the song type he called a "lyrical subsong", probably a female.

Tape recordings were obtained from the Cornell Laboratory of Ornithology of two individuals of *zena* on New Providence. In the first, lasting 2 min., there was a series of 17 short songs, each from 1.5 to 3.5 sec. in length, alternating with 2 to 6 sec. pauses. In sonograms of three of the short songs (Fig. 3A,B,C) most of the sounds were thin, squeaky, de-

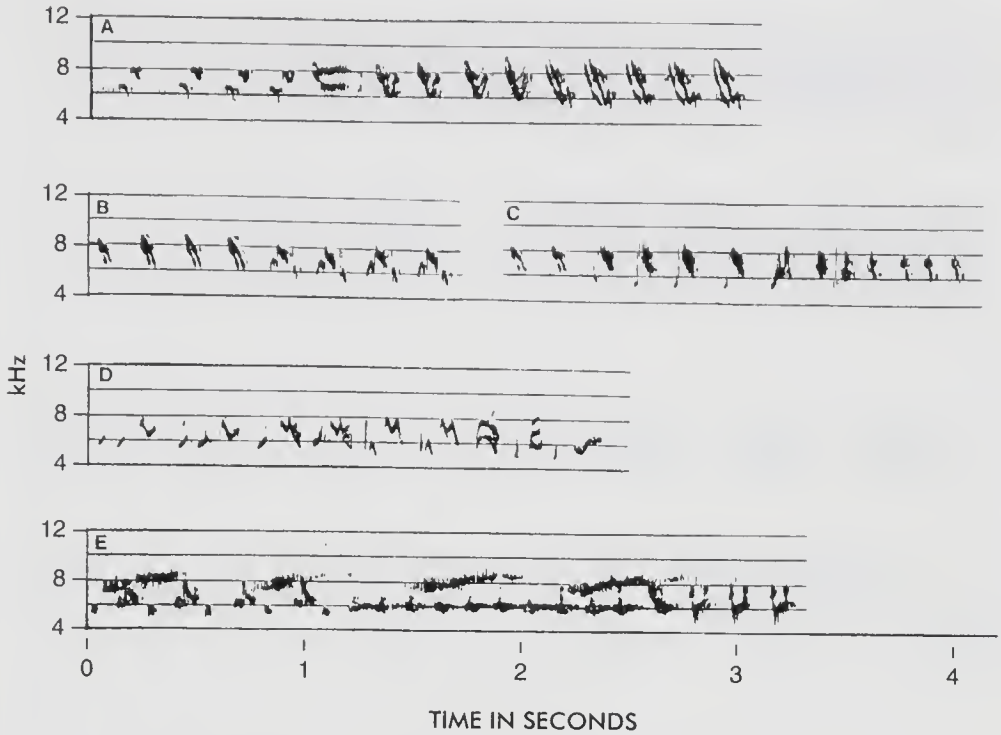

FIG. 3. Vocalizations of *Spindalis zena zena* (see text).

scending-pitch "*slurs*" along with two to four note syllables. Although there were several different types of vocalizations, they were each given with little change and without any resulting rhythmic pattern. One (Fig. 3C) showed a slight increase and decrease in intensity.

Sonograms were made from a 3 min. 45 sec. song session from a second individual, of four short songs included in that session (Fig. 3D,E, and Fig. 4A & B). In the latter two, the second line is a continuation of the first line in that sonogram. This individual's singing was similar to that in Figs. 3A to C in having short songs, short pauses, and grouping of a few different syllables, each replicated a few times. The second bird differed in using more complicated syllables and particularly in using them to make rhythmic groupings. The versatility of song types is again evident, creating new syllables in each short song, not duplicating exactly any previous syllables.

In one short song (Fig. 3E) sounds around 8 kHz and others around 6kHz suggest that this is a form of "duetting", from a double syrinx. This is also evident in another section from the same song (Fig. 4A), to be discussed below.

Cuba.—Songs from the birds in Cuba are very thin, high-pitched notes, which might be confused with those of the Cuban Bullfinch (*Melopyrrha nigra*). Among the three birds whose songs were recorded, each had a different set of notes, phrases, and patterns of delivery. A male used the

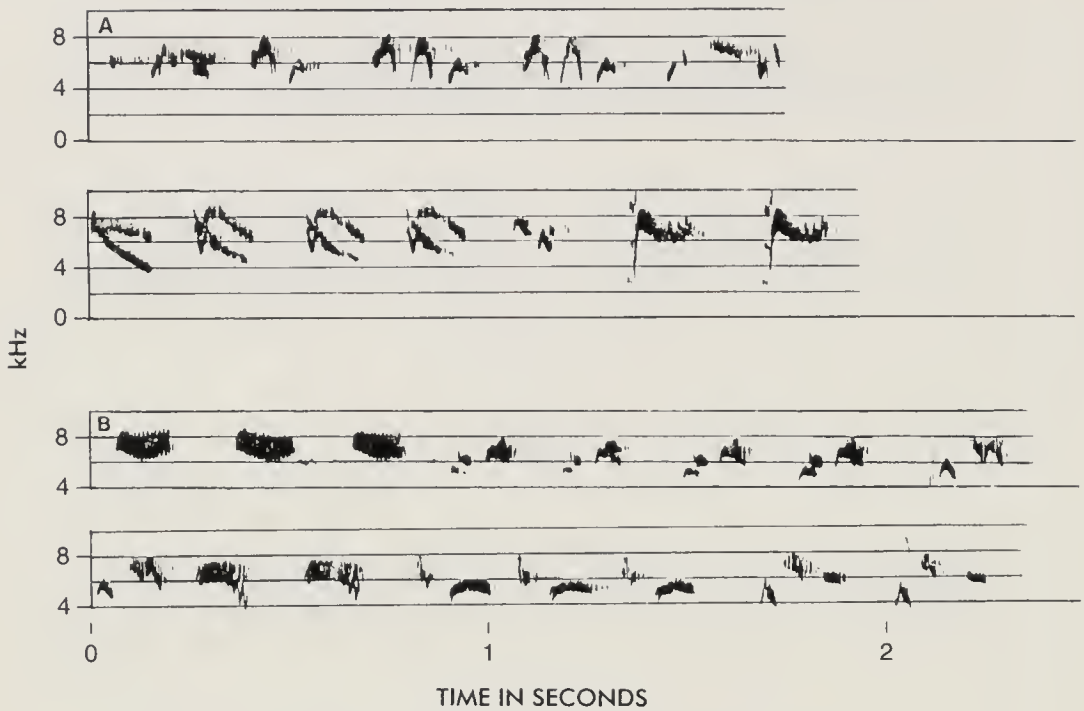

FIG. 4. Vocalizations of *Spindalis zena zena*, continued (see text).

short song, short pause pattern (Fig. 5B), delivering 17 short songs in a 37 sec. series with similar phraseology and rhythmic form.

A second bird, of undetermined sex, sang hidden in dense undergrowth, using 6–7 sec. songs alternating with 4–5 sec. pauses (Fig. 5A). It used everchanging, sibilant, thin, discrete notes, without any clear rhythmic form. A fast twitter is found in the middle of the area shown.

In the third bird, the source was again not in view, but this is a "whisper song" type of performance (Fig. 5F), believed to be from a female. It used a less common low frequency, ca. 2 kHz, initially with groups of similar syllables of notes during an 11 sec. song session. The sonogram is from a tracing of the original, which included a heavy chorus of sounds from amphibians and insects, and the high complexity in the 3rd and 4th secs. is of uncertain sources; a second tanager may have joined in for a duet, and the marks over 8 kHz may be from an insect!

Three males are responsible for the additional calls here. The weak "tsee" (Fig. 5C) was later given as a double "tsee tsee" covering less than 0.2 sec., A more intense "chip" (Fig. 5D) was used during feeding activities, and the more prolonged "seee" (Fig. 5E) was used in a long series, prior to the start of a song session.

Jamaica.—Previous authors have not been impressed by the vocal performances of *Spindalis* in Jamaica. Gosse (1847) wrote "during flight, a low sibilant note is uttered; but it is usually a silent bird." Lady Taylor

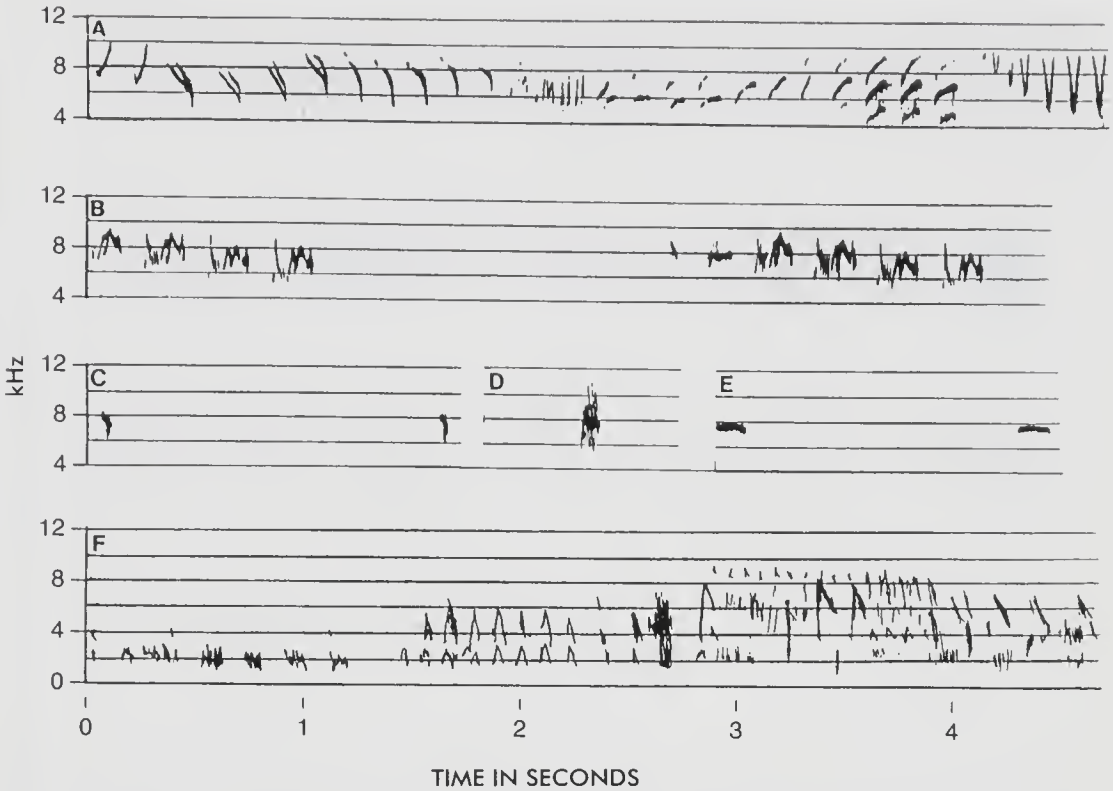

FIG. 5. Vocalizations of *Spindalis zena pretrei* (see text).

(1955) described "a crowd of as many as eight or ten of these beautiful birds. . .feeding with much chattering and scolding on fruits of a single tree. . .like many other tanagers it has no true song." Jeffrey Smith (1956), a lifelong resident of Jamaica, wrote of *Spindalis* "It is no songster and both the male and his mate are usually silent, but in the courting season I have heard the female sing. . .When gathering material for a nest a harsh 'chrruky' note is uttered." Most recently, Downer and Sutton (1990) stated that the voice of *Spindalis* in Jamaica is a "very soft 'seep' often given in flight, and other high, fast 'chi-chi-chi-chi-chi' notes."

In contrast with the unenthusiastic reports on this tanager's singing, Sutton, in March 1995, recorded a male with a 2 min. 20 sec. "dawn song" from high in a tree top! The distinctive performance used intense, tremulous whistles, with 7–11 syllable phraseology, like that from another male in an earlier recording (Fig. 8A). This group of whistles was given every 6–7 secs., and during the second min. of the song, several faster pulsating vocalizations were inserted, like those from another previous male recording (Fig. 7A). Also inserted were several "séaas" (Fig. 8E) in the same 8 kHz range as the song.

Our survey supports the fact that females do sing; those we taped have been classified as weak "Whisper songs." One female in a 3 min. 40 sec.

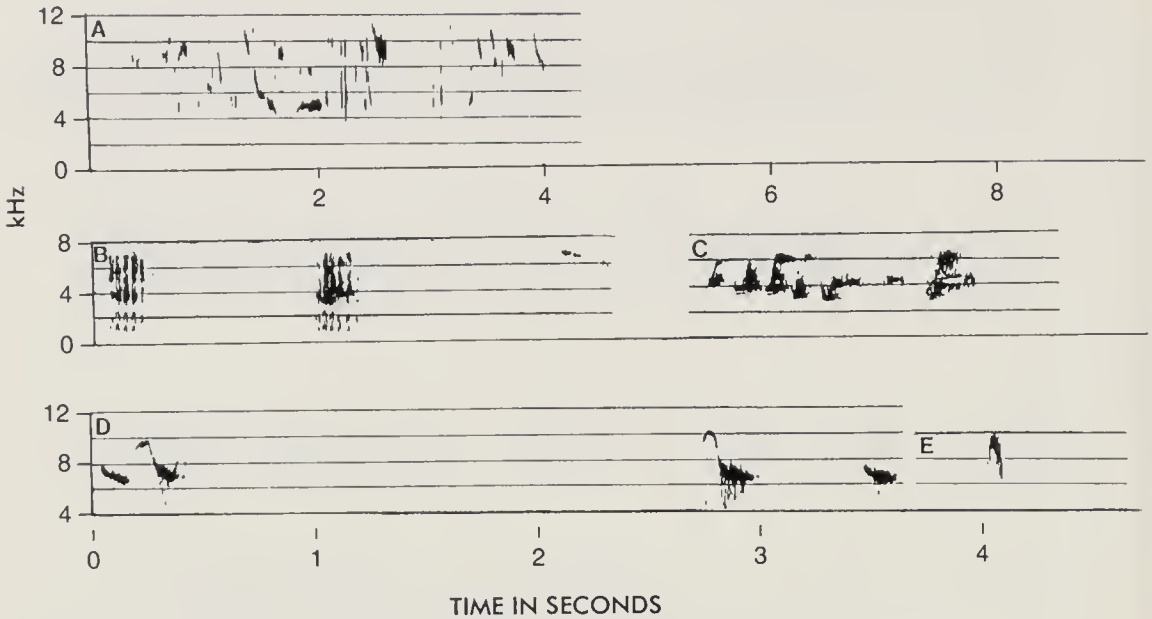

FIG. 6. Vocalizations of *Spindalis nigricephala* (see text).

performance used rhythmic short songs (Fig. 6A), some 50 times, alternating with short pauses, and included various squeaks and whistles. A second example, in this same song session (Fig. 7A) shown in an ex-

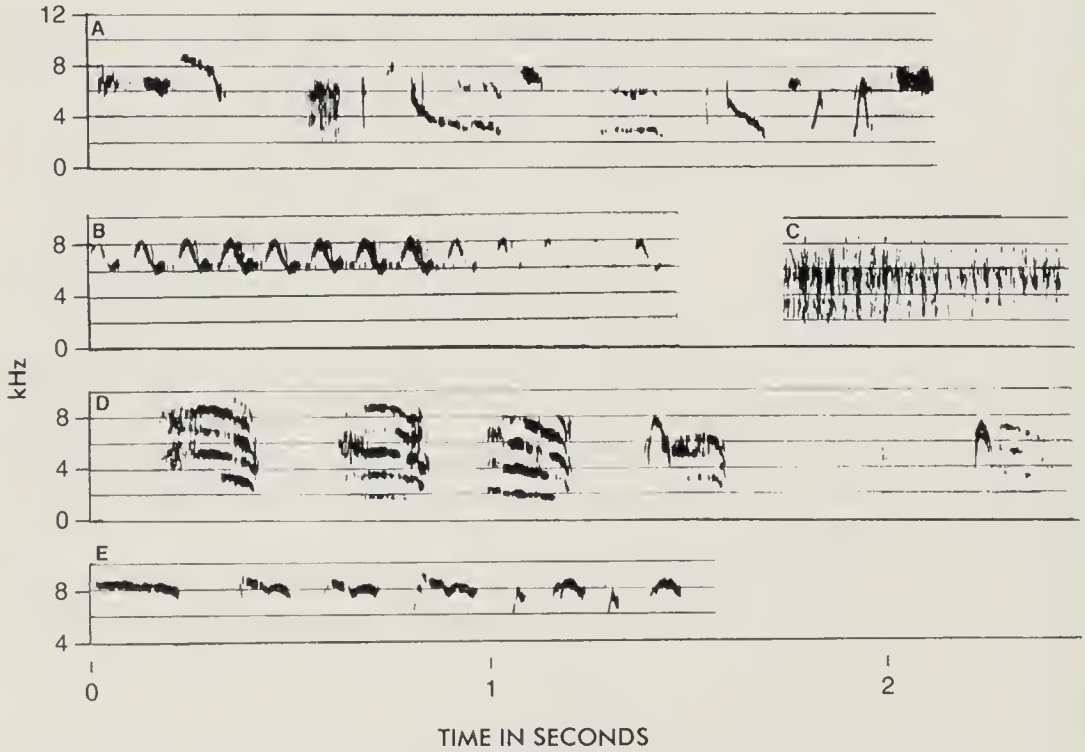

FIG. 7. Vocalizations of *Spindalis nigricephala*, continued (see text).

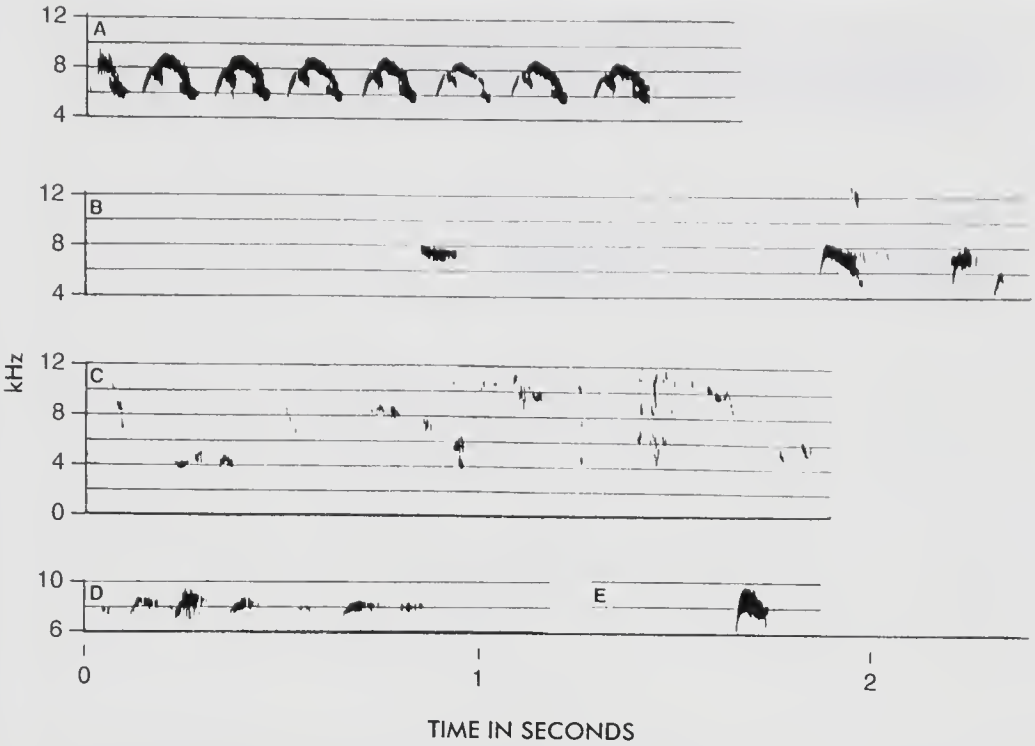

FIG. 8. Vocalizations of *Spindalis nigricephala*, continued (see text).

panded time scale, shows again the continuing variation in types of notes and phrases as well as great changes in pitch.

In a second "whisper song" from a female at Marshall's Pen, Mandeville (Fig. 8C) there were everchanging notes and syllables in 1–2 sec. short songs, and 4–8 sec. pauses, and no rhythmic groupings. The bird was in a dense thicket, less than 0.5 m from the ground, singing so quietly that it was barely audible from a distance of 4 m, but was recorded using an 81 cm diameter parabolic reflector. Just prior to the song, it had uttered two "churrs" (Fig. 6B) and a rhythmic phrase "see seea chi lo" (Fig. 8B).

A number of miscellaneous calls are on hand, some of ours and others from outside sources, with only a few with known context, with notes accompanying the recordings. A stuttery series (Fig. 6C) appeared to have two sources, either two individuals or one individual using the two syringes; two forms of "seeps" may have been from two interacting individuals (Fig. 6D); a dry chatter (Fig. 7C) from a mostly hidden feeding group; distress notes (Fig. 7D) from a male being removed from a mist net; somewhat rhythmic high-pitched squeals (Fig. 7E) during a quick fly-off from a perch, and finally, rhythmic phrases (Fig. 8D) from a female in a mixed flock.

Among the 15 sonograms from Jamaica (Figs. 6,7,8) three are from one female (Figs. 6B, 8B & 8C), the remainder from 12 different birds.

Grand Cayman.—Of the Grand Cayman race *salvini,* Bradley (1985)

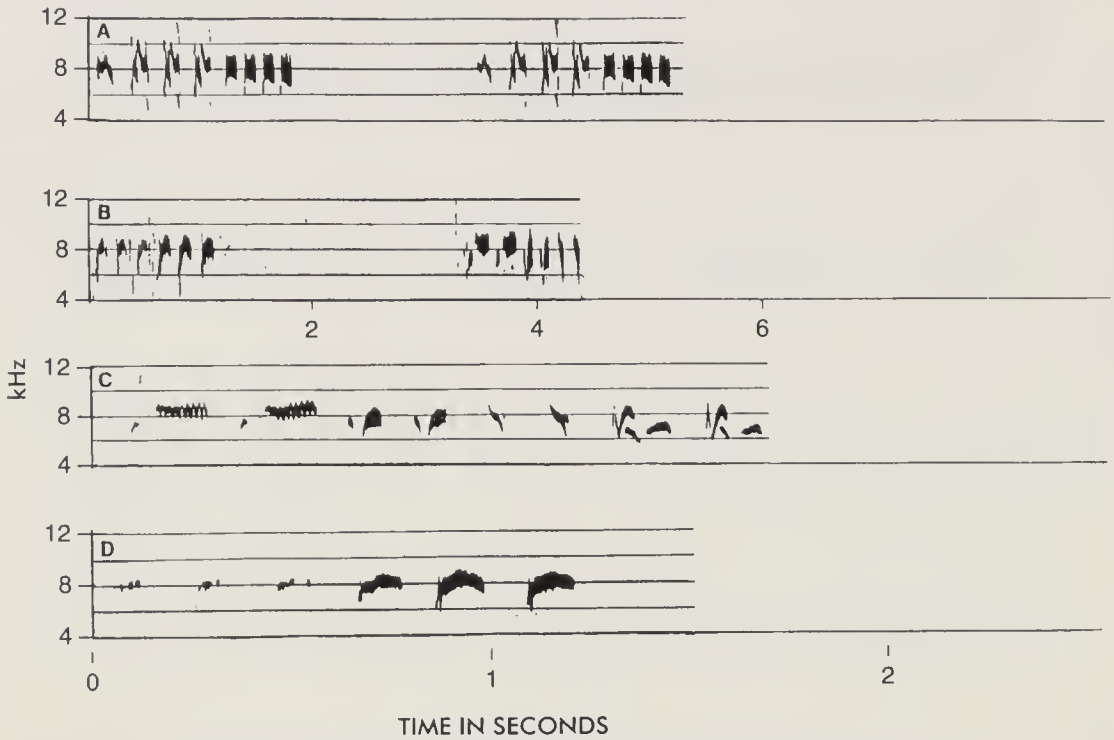

FIG. 9. Vocalizations of *Spindalis zena salvini* (see text).

wrote "Call *tweep* and a pretty mewing warble, 8 to 9 syllables rising then falling; sings constantly in spring and throughout the summer."

Recordings were obtained from two male birds, each using the short song, short pause pattern, with rhythmic phraseology. From the first, the singing emphasized terminal phrases or notes, as shown in three sonograms, during a 3 min. session (Figs. 9A, 10A, 10B). The first song in Fig. 9A is repeated in an expanded time sonogram (Fig. 10C) giving a clearer picture of the individual phrase structure. It is of interest that emphasis at first was in the 8 kHz range, dropping to 4 kHz in the 2nd and 3rd sonograms. A slight rise and fall in pitch was found in Fig. 9A.

A second bird, singing sporadically over a 3 min. period, kept inventing new notes and phrases, a common practice in all but the Puerto Rican populations, introducing them as duplicate or triplicate phrases (Fig. 9B, C, D). In the last, with the extreme loudness change, it may be that the bird turned, singing "away from" to "toward" the recordist, or else it was changing from a weak to a loud delivery. In the second song example (Fig. 9C), this pattern may be the "mewing warble" of Bradley's description above.

Cozumel Island, Quintana Roo, Mexico.—Ludlow Griscom spent three days in February 1926 on Cozumel Island, and reported (Griscom 1926) that he "did not find the present species [which he called *Spindalis benedicti*] at all common . . . It was not in song and not breeding, however,

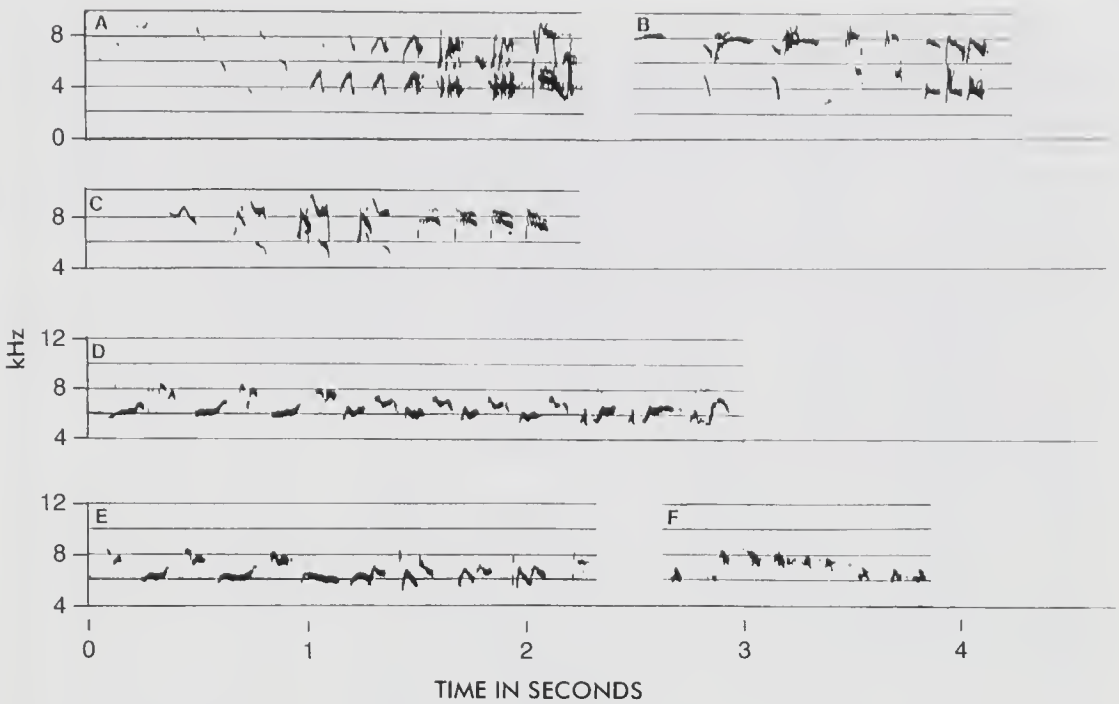

FIG. 10. Vocalizations of *Spindalis zena salvini* continued (A, B, C), and *S. z. benedicti* (D, E, F; see text).

which may in part account for its apparent scarcity." Griscom must have been looking in the wrong habitats, as Parkes and his colleagues had no difficulty in finding non-breeding flocks of *Spindalis* on Cozumel in January and November 1965, and there is no evidence of major habitat changes on Cozumel between 1926 and 1965. Griscom described "the call-note" as "a weak, reedy lisp, suggesting notes of various species of *Chlorospingus*." Edwards (1972) described the song of *benedicti* as "an extremely high-pitched, chippering, chattering series of notes." Howell and Webb (1995) characterized the song as "a high, thin, twittering *tsi-si-tsi-si-si-i-tsi-si-si-i si-i*, with increasing intensity. Calls a high, thin to slightly shrill *tssi* and *tssi-ssi-ssi*, suggesting a *Turdus* flight call."

Only one territorial song performance was available from Cozumel Island. This is a 1 min. 38 sec. session, with 2 to 4.5 sec. short songs, alternating with 3-4 sec. pauses. The songs were rhythmic and almost every different syllable appeared in duplicate, triplicate, or more replications (Fig. 10D, E).

It is of interest that the two songs, as well as most of the other 12 songs in this performance, had similar phraseology in the first second of the song, each continuing with its own variations.

In a second recording, a male used "short spurts of calls" (Fig. 10F) when displaying in flight to another bird. There were also noises from wing and tail feathers beating on air, not detected in the sonogram.

Vocalizations: discussion.—A review of the sonograms shows wide variations in many factors, including pitch, speed of delivery and types of notes or of complex syllables or phrases. We lack any long time-period tapes, e.g., 1–2 years, from any one individual, in a far from complete tape collection. Only one song series was obtained from Cozumel Island (Fig. 10D, E), and only two individuals from the Bahamas; the first (Fig. 3A, B, C) and the second (Fig. 3D, E, & Fig. 4A, B), both from *S. z. zena* and none from *S. z. townsendi*. The tapes assembled, however (Table 3), from male songs in seven locations, have given us some insight into the inter-island relationships.

One of the most distinctive male vocalizations is from Jamaica, evaluated from selected sonograms, during a recently recorded dawn song (Table 3, Figs. 8A and 7B). These are not like any other vocalizations heard or taped from other populations of *Spindalis*, supporting separate species designation for *nigricephala*. In addition, two whisper songs from females in Jamaica (the first, Figs. 6A, 7A; the second, Fig. 8C) are each quite different from whisper songs from females in Hispaniola (Fig. 2C) and Cuba (Fig. 5F).

A second distinct vocalization from males, heard in Puerto Rico (Table 3, Fig. 1A), uses short notes in both 7 kHz and 9 kHz pitch levels, to form a rhythmic song pattern. This is repeated, accurately and regularly, as a dawn song, and often at other times of day. Additional information on this population was provided by Dr. Joseph Wunderle, Jr. (in litt.), who stated that he had never heard the "high-pitched, fast warble" type of singing from Stripe-headed Tanagers in Puerto Rico.

A third distinct male song is heard in Hispaniola, recorded in the eastern (Dominican Republic) section of the island (Table 3, Fig. 2A). The dawn song uses simple, sibilant notes, similar overall to those in Puerto Rico (above), but differing as follows: in Hispaniola the song unit uses 4 similar "seeps" at one pitch, ca. 8 kHz, whereas in Puerto Rico the unit uses nine "seeps", of three types, rhythmically in two pitches, at ca. 7 and 9 kHz.

In contrast with the simple notes in the male songs from the three locations described above, complex syllables and changing phraseology are the rule in the Bahamas, Grand Cayman, and Cozumel Island (Table 3). The sonograms are clearly different visually, as well as in hearing songs in the field. Although we do not have numerous recordings, those figured here are believed to be typical in each population.

The fourth population different from the Jamaica, Puerto Rican and Hispaniolan *Spindalis* in its vocalizations is that in Cuba (Table 3). This has complex syllables like those in the Bahamas, Grand Cayman, and Cozumel, but repeats the same syllable type instead of having ever-chang-

TABLE 3

REPRESENTATIVE VOCALIZATIONS FROM FIGS. 1–10 CURRENTLY CONSIDERED TO BE MALE TERRITORIAL SONGS

Country	Figure	Comments	Location, date, recordist
Puerto Rico	1A	The song unit is 3 sets of these 3 syllable phrases given rhythmically and repeated every 6–7 secs.	Maricao, 20 Apr 1962 G. B. Reynard
Dominican Republic	2A	The song unit is 4 of these notes, closer together, in a rhythmic pattern, paraphrased (Wetmore 1931) as "tsee see see see"; confirmed by J. Wunderle, Jr. (in litt.).	Cotui, 8 Mar 1969 G. B. Reynard
Jamaica	8A, 7B	Two examples of the fast, intense, pulsating warbles during an early morning treetop song.	Hardwar Gap, 16 May 1995 R. L. Sutton
Bahamas (New Providence)	3A, B, C	Three parts of a short song, short pause delivery; fast, non-rhythmic, frequent syllable changes, given in a more or less "recitative" manner.	Prospect Ridge, 28 May 1971 P. A. Dean & P. P. Kellogg
Cuba (Pinar del Rio Prov.)	5B	Part of a short song, short pause session, with repeated use of the same phrase pattern (a second individual of undetermined sex [Fig. 5A] used ever-changing notes).	La Guira, 5 May 1976 G. B. Reynard
Grand Cayman	9A, 10A, B	Four rhythmic short songs with simple notes and complex syllables and terminal note group emphasis.	Georgetown, 3 June 1969 G. B. Reynard
Mexico (Cozumel Is.)	10D, E	Two of 13 short songs, most of which used the same initial notes, then all new, often repeated, low-higher syllables.	El Cedral, 20 Mar 1979 R. B. Waide

ing syllables. We have only this one male vocalization (Fig. 5B), and it follows the short song, short pause pattern.

Although the Puerto Rican and Hispaniolan territorial songs were clearly different, as described above, one call was found to be common to both islands. This was the "twitter" (Puerto Rico, Fig. 1B; Hispaniola, Fig. 2B); these are sonograms shown at two different time scales, but the sounds are essentially identical in pitch and pattern.

Another helpful report from Dr. Wunderle (in litt.) stated that *Spindalis* in both Hispaniola and the Caymans is "very different" from the birds in Puerto Rico—this referring to morphology.

Although we do not have any evidence of mimicry in *Spindalis*, its innovative phraseology, notes, or syllables challenge the degree of versatility in songs of the Northern Mockingbird (*Mimus polyglottos*)! An interesting feature of *Spindalis* songs is the ability to produce from the dual syrinx two different sounds simultaneously, an ability reviewed by Gill (1989) for several other species. Sonograms showing this feature are as follows: Fig. 3A, B, C in the Bahamas and, from a second Bahaman bird, Figs. 3F and 4A, second line; Fig. 5A from Cuba, and questionably Fig. 6C, cited earlier, which may have been from two individuals, in Jamaica.

The analyses of the vocalizations from the seven geographical areas support the morphological information on which the taxonomic arrangement proposed in this paper is based.

Natural History

The available information on the behavior, trophic niche, nesting, and foraging habits of the various forms of *Spindalis* is relatively scant. Isler and Isler (1987) assembled information on these matters from the available literature; their summaries need not be repeated here. Their taxonomic treatment follows Storer (1970) in keeping all forms of *Spindalis* in the single species *zena*, but they arrange their text into three "subspecies groups" that correspond to the three species recognized by Steadman et al. (1980). Like several other authors, they erroneously use the junior name *dominicensis* instead of *portoricensis* for what they call the "Eastern Stripe-headed Tanager."

Comparisons of life history information as presented from the literature by Isler and Isler (1987) offer few distinctions among the taxa of *Spindalis*, and some of the apparent differences may simply be based on insufficient observations. Authors generally agree that these tanagers are primarily frugivorous, eating both berries, that are swallowed whole, and large fruits which are torn open to get at the pulp. Isler and Isler cite insectivory only for *dominicensis* and *portoricensis*. Wetmore (1927) and

Brudenell-Bruce (1975) described feeding on tender young leaves by *portoricensis* and *zena*, and the Suttons have seen *nigricephala* commonly feeding on leaves, even mature ones, in Jamaica. Wetmore and Swales (1931) mention "seeds, berries and fruits of various kinds"; the anecdotal accounts they cite all involved berries. Parkes's observations of *benedicti* on Isla Cozumel agree with those of Wetmore and Swales who recorded *dominicensis* "traveling at times to congregate in abundance where some fruit is ripening."

No in-depth life history studies of these tanagers appear in the existing literature, but Raúl Pérez-Rivera is presently engaged in making life history studies of *Spindalis* in Puerto Rico.

There are only a few descriptions of the nests and eggs of *Spindalis*, and none at all of some taxa. Authors agree that the nest is cup-shaped, composed of various kinds of plant materials. Bond (1936) summarized the measurements of eggs of four of the taxa as follows: *nigricephala*, 24 × 18 mm; *dominicensis*, 22 × 15 mm; *salvini*, 23.5 × 16.5 mm; and *portoricensis*, 25 × 17 mm. Wetmore (1927) measured two eggs of the latter at 23.7 × 18.2 and 24.2 × 18 mm. Pérez-Rivera (MS) gives the average measurement of 16 eggs of *portoricensis* as 23.7 × 17.3 mm. Gundlach (1893) gave egg measurements for Cuban *pretrei* as 22 × 15 mm. Despite the much larger body size of *nigricephala*, there is very little difference in egg size among these taxa.

Egg color is highly variable according to Bond (1936): "pale bluish green, marked with pale grayish brown and more or less scrawled with black about the larger end, or spotted chiefly about the larger end with brown, or brown and lilac, or heavily spotted, scrawled and marbled with various shades of brown and lavender." Unfortunately, it is not clear whether the variation described by Bond is within a single taxon or for the whole group collectively. Gundlach (1893) described the eggs of *pretrei* as white with isolated spots, the larger darker, the smaller brown. Ogilvie-Grant (1912) described the eggs of *nigricephala* as follows: "In two eggs the ground-color is greenish-white heavily marked and blotched all over with burnt-umber and with underlying spots and blotches of paler greyish-brown, the markings being thickest toward the larger end, where they almost obscure the ground-color . . . In a third egg the markings, which are much smaller and less numerous, are reddish-brownish and reddish lilac." The only recent description of egg color in *Spindalis* that we have seen is that of Pérez-Rivera (unpubl. data), writing of *portoricensis*. He agrees that the color and pattern of markings is highly variable, which makes it clear (as Bond did not) that this variation exists within a single island population as well as across the genus *Spindalis*. It would be necessary to examine large numbers of eggs of all of the taxa to

determine whether geographic variation transcends individual variation in egg color.

Taxonomic Conclusions

To review the vocal evidence, the recordings of Reynard (1969, 1981) indicate that the morphological distinctness of Puerto Rican *portoricensis* and Hispaniolan *dominicensis* is reflected in the differences in their vocalizations. The populations of the *zena* group (including *pretrei, townsendi, salvini*, and *benedicti*) have the most elaborate songs, that of *portoricensis* is less elaborate, and *dominicensis* even less so. The Jamaican *nigricephala* has a rattling note unique in *Spindalis*, and flight song has been described only for Bahaman and Cozumel birds; the observations of Brudenell-Bruce were made on New Providence and thus refer to *zena*.

After consideration of all available comparative data on measurements and weights, color and pattern (especially of females), voice, and distribution, we believe it is unrealistic to regard all forms of *Spindalis* as comprising a single species, *S. zena*. The A.O.U. Check-list (1983) mentions (p. 652) that "some authors have suggested that three species should be recognized, *S. dominicensis* (Bryant, 1866 [error, =1867]) from Hispaniola, Gonave Island and Puerto Rico, *S. nigricephala* (Jameson 1835) from Jamaica, and *S. zena* in the remainder of the range . . ." This suggestion was probably taken from the footnote comment of Bond (1956), who listed all *Spindalis* as races of *zena*, but stated that the three-species treatment might be "more satisfactory."

The treatment we recommend is essentially that of Bond (1945), but with four species constituting a superspecies (although Bond did not use the latter word). The taxa are as follows (plumage characters are given earlier in this paper and measurements on Table 1):

Spindalis zena (Linnaeus), 1766

NORTHERN STRIPE-HEADED TANAGER,
with five subspecies as follows:
Spindalis z. pretrei (Lesson), 1831

Tanagra Pretrei Lesson, Cent. Zool., 1831, p. 122 (Brésil; error, = Cuba).

Synonym: *Spindalis pretrei pinus* Bangs and Zappey, Amer. Nat. 39, 1905, p. 213 (Santa Fé, Isle of Pines).

Inhabits Cuba, the Isle of Youth (formerly Isle of Pines), and numerous keys off Cuba, including Cinco Leguas, Conuco, Francés, Las Brujas, Santa María, Guillermo, Coco, Paredón Grande, Romano, Guajaba, and Sabinal on the north coast, and Cantiles on the south coast. The color characters of the alleged race *pinus* from the Isle of Pines prove to be based on seasonal variation and the measurement differences are trivial.

Spindalis z. salvini Cory, 1886

Spindalis salvini Cory, Auk 3, 1886, p. 499 (Grand Cayman)

Endemic to the island of Grand Cayman (not yet recorded from any other island in the Cayman group).

Spindalis z. benedicti Ridgway, 1885

Spindalis benedicti Ridgway, Proc. Biol. Soc. Washington 3, 1885 (March), p. 22 (Cozumel [Island]), Yucatan.

Synonym: *Spindalis exsul* Salvin, Ibis 1885 (April), p. 189 (Cozumel Island).

Endemic to the island of Cozumel, Quintana Roo, off the east coast of the Yucatán Peninsula, Mexico.

Spindalis z. townsendi Ridgway, 1887

Spindalis zena townsendi Ridgway, Proc. U. S. Nat. Mus. 10, 1887, p. 3 (Abaco).

Inhabits Grand Bahama, Great Abaco, Little Abaco, and Green Turtle Cay islands in the northern Bahamas.

Spindalis z. zena (Linnaeus), 1766

Fringilla zena Linnaeus, Syst. Nat., ed. 12, 1766, p. 320 (Bahama Islands = New Providence).

Inhabits the central and southern Bahama Islands, from the Berry Islands south to Great Inagua, and Providenciales (only) in the Turks and Caicos Islands (Buden 1987).

Spindalis portoricensis (Bryant), 1866
PUERTO RICAN STRIPE-HEADED TANAGER

Tanagra portoricensis Bryant, Proc. Boston Soc. Nat. Hist. 10, 1866, p. 252 (Puerto Rico).

Endemic to the island of Puerto Rico.

Spindalis dominicensis (Bryant), 1867
HISPANIOLAN STRIPE-HEADED TANAGER

Tanagra dominicensis Bryant, Proc. Boston Soc. Nat. Hist., 11, 1867, p. 92 (Southeast Haiti).

Endemic to the island of Hispaniola and adjacent Gonave Island. Dod (1978) states that there is geographic variation in color in the Dominican Republic, but we have not had the opportunity to investigate this.

Spindalis nigricephala (Jameson, 1835)
JAMAICAN STRIPE-HEADED TANAGER

Tanagra nigricephala Jameson, Edinburgh New Philos. Journ. 19, 1835, p. 213 (Jamaica).

This species is endemic to the island of Jamaica. Hellmayr (1936) gave *S. bilineatus* Jardine and Selby, 1837, and *Tanagra zenoides* Des Murs, 1847, as synonyms; we have not checked these references, as both names are junior to *nigricephala*. Hellmayr also stated that *Fringilla cana* Gmelin, 1789, might be an earlier name for this species, in which case it would replace the junior *nigricephala*. However, Hellmayr found discrepancies in the descriptions on which Gmelin's name was founded and consequently declined to adopt the latter.

DISCUSSION

To some extent, the sequence of species and subspecies adopted is arbitrary. There is no evidence on which to base conjecture as to the

characters of the ancestral *Spindalis*. The amount of differentiation can be a clue as to the length of time that the populations of individual islands have been isolated from other populations. Within the *zena* group, the populations of the Cuban keys and of the Isle of Youth have not been sufficiently isolated in time, space, or both to have differentiated from *pretrei* of mainland Cuba. The same point could be made about populations of the various Bahaman islands occupied by *zena* and *townsendi*, and in fact there is evidence for gene flow between those two subspecies. The Gonave Island population of *dominicensis* has not become differentiated.

The peripheral ranges of *zena* and *townsendi* in the Bahamas, *salvini* on Grand Cayman, and *benedicti* on Isla Cozumel suggest that all of these races of the *zena* group probably originated from invasions from Cuba. The histories of the other species are harder to hypothesize, other than that the distinctness of *nigricephala* suggests a long isolation on Jamaica. For these reasons, we place the Jamaican species *nigricephala* last in the sequence, and the polytypic species *zena* first, beginning with the probable core form, the Cuban *pretrei*. The two species with streaked females, *portoricensis* and *dominicensis*, occupy an intermediate position, but the distinctiveness of the males of both species precludes any deduction as to relationships with each other or with taxa within the genus.

Nedra Klein has studied this genus from the aspect of molecular genetics (pers. comm.) In general, her findings match ours, in that *portoricensis, dominicensis*, and *nigricephala* are all strongly differentiated. She found that the birds of the Bahamas diverged somewhat from the others that we include in the species *Spindalis zena*, and thus she prefers to recognize five species rather than four; the fifth species would take the name *Spindalis pretrei*, and would include *pretrei, salvini, benedicti*, and *townsendi*. However, there is no "rule" that specifies the extent of genetic differentiation required for the recognition of a taxonomic species, and the mtDNA data analyzed in so many recent papers "represent a single gene tree that is embedded in the organismal phylogeny" (Zink et al. 1995), i.e., conclusions are being drawn on the basis of comparisons of a minute fragment of the bird's total genome. In view of the strong morphological resemblances within the northern populations and the distinctiveness of the Jamaican, Hispaniolan, and Puerto Rican populations, we prefer to unite the former in a single polytypic species, *S. zena*.

The only other published study of molecular genetics in West Indian birds of which we are aware is that of Klein and Brown (1994) on the Yellow Warbler (*Dendroica petechia*). This study differs fundamentally from that of *Spindalis* in that the warbler is widely distributed on the

mainland as well as on non-West Indian islands, and its history may involve multiple invasions.

As is well known, the definition of genera in ornithology is highly subjective and subject to change with alternating popularity of "lumping" and "splitting." Bond's most recent work, the 5th edition of his field guide (1985), included 44 genera endemic to the West Indies. The recent world list of Sibley and Monroe (1990) reduces this list to 36, plus three that have only recently been combined with larger, extra-Antillean genera ("*Tolmarchus*" = *Tyrannus*, "*Lamprochelidon*" = *Tachycineta*, and "*Mimocichla*" = *Turdus*). These genera can be divided into several categories. Of these, 13 are monotypic genera containing a single monotypic species inhabiting only one island (except *Cyanophaia*, which occurs on both Dominica and neighboring Martinique). Few West Indian genera are clearly polytypic, with species status made clear by sympatry; these include *Todus, Margarops*, and *Loxigilla* (formerly on St. Kitts; *L. portoricensis* now extinct there). Most of the endemic genera include a single polytypic species or superspecies, with the distinction not always clear (as has been the case with *Spindalis*). The lizard-cuckoo genus *Saurothera* provides the nearest parallel to *Spindalis*, as it contains two monotypic and two polytypic species (Bond 1956); however, the morphological and vocal differences among *Spindalis* species are more pronounced than in *Saurothera*.

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EDITOR'S FAREWELL

This issue ends a decade during which I processed more than 2,000 manuscripts, published more than 8,000 pages and interacted with hundreds of referees and authors. It was an entirely positive experience and I owe the members of the Wilson Ornithological Society thanks for their generosity and support throughout my editorship.

I am indebted especially to Kathy Beal, Al Conway, Ted Davis, and George Hall for their outstanding service in producing the bulletin. Karen Blem Killeen and Robert Blem provided outstanding office support at critical times. Numerous "super-referees" and editorial board members were instrumental in judging the quality of submissions. I particularly thank Richard Conner, Tom Haggerty, Chris Stinson, and Clait Braun for their reviews of numerous manuscripts. I apologize to those people to whom I do not here pay tribute. There were so many who did large and small favors for the bulletin that I could not comprehensively recognize all of you.

Finally, I thank Leann Blem for her tireless, unpaid service for the past ten years. She read manuscripts, edited my prose, typed responses to authors, selected referees, kept me organized, and generally was responsible for any success the journal may have had during the period. I am lucky, indeed, to have her for my wife, partner, and colleague.

Our goal throughout our tenure was to move the journal a bit ahead of its status when we assumed the duties of editing it. I hope that you agree that we did that. Many thanks.

C. R. Blem

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LONG-TERM DYNAMICS OF BIRD COMMUNITIES IN A MANAGED FORESTED LANDSCAPE

RICHARD H. YAHNER[1]

ABSTRACT.—I examined the long-term dynamics of wintering and breeding bird communities at the Barrens Grouse Habitat Management Area (HAM) in central Pennsylvania. I compared community structure (species richness and population abundances) among three forested sectors that varied in extent of clearcutting and among forested plot types of different age since clearcutting from 1993–95 (termed period 2). These results, which were obtained six–eight years subsequent to a third cutting cycle, were then contrasted to those from a previous study (1988–90, termed period 1). The Barrens Grouse HMA consisted of three distinct sectors: a contiguous uncut stand, a series of uncut strip corridors, and a mosaic of small (1 ha) forest patches (plots). I observed 12 wintering bird species in period 2; most species (67%) were trunk-bark foragers. Uncut plots were used more often ($P < 0.05$) by wintering birds than clearcut plots, perhaps because uncut plots contained rough-barked trees as foraging substrate and more favorable microclimatic conditions. Of the 40 breeding bird species noted in period 2, most were ground-shrub foragers occurring principally in forested corridor and patch sectors. Abundances of six ground-shrub foraging species were higher ($P < 0.05$) in the forested patch than in other sectors in period 2; these species were found primarily in recent clearcut plots. Abundances of sallier-canopy foragers were higher ($P < 0.05$) than expected in contiguous forest and forested corridor sectors in period 2. Species richness, abundances of all wintering species combined, and abundances of two foraging guilds (trunk-bark and ground-shrub foragers) were similar among scctors in periods 1 and 2 in both winter and the breeding season. Abundances of three wintering species, however, were greater ($P < 0.05$) in period 2 than in period 1. In contrast to winter, abundances of all breeding species combined, sallier-canopy foragers, and five species increased ($P < 0.05$) between periods, whereas abundance of three species declined. Significant changes in abundances of wintering and breeding birds between periods at the Barrens Grouse HMA may be explained partially by plant succession or regional trends in population abundances.
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The effect of even-aged management on abundance and distribution of bird communities has been examined in various managed forested landscapes (e.g., Crawford et al. 1981, Thompson et al. 1992, Welsh and Healy 1993). In this study, I examined the long-term dynamics of wintering and breeding bird communities at the Barrens Grouse HMA in central Pennsylvania subsequent to a third cutting cycle. My objective was to compare community structure among three forested sectors that varied in extent of clearcutting and among plot types of different age since clearcutting from 1993–95, which was six–eight years following the third cutting cycle (termed period 2). In addition, I contrasted results

[1] School of Forest Resources, The Pennsylvania State Univ., University Park, Pennsylvania 16802.

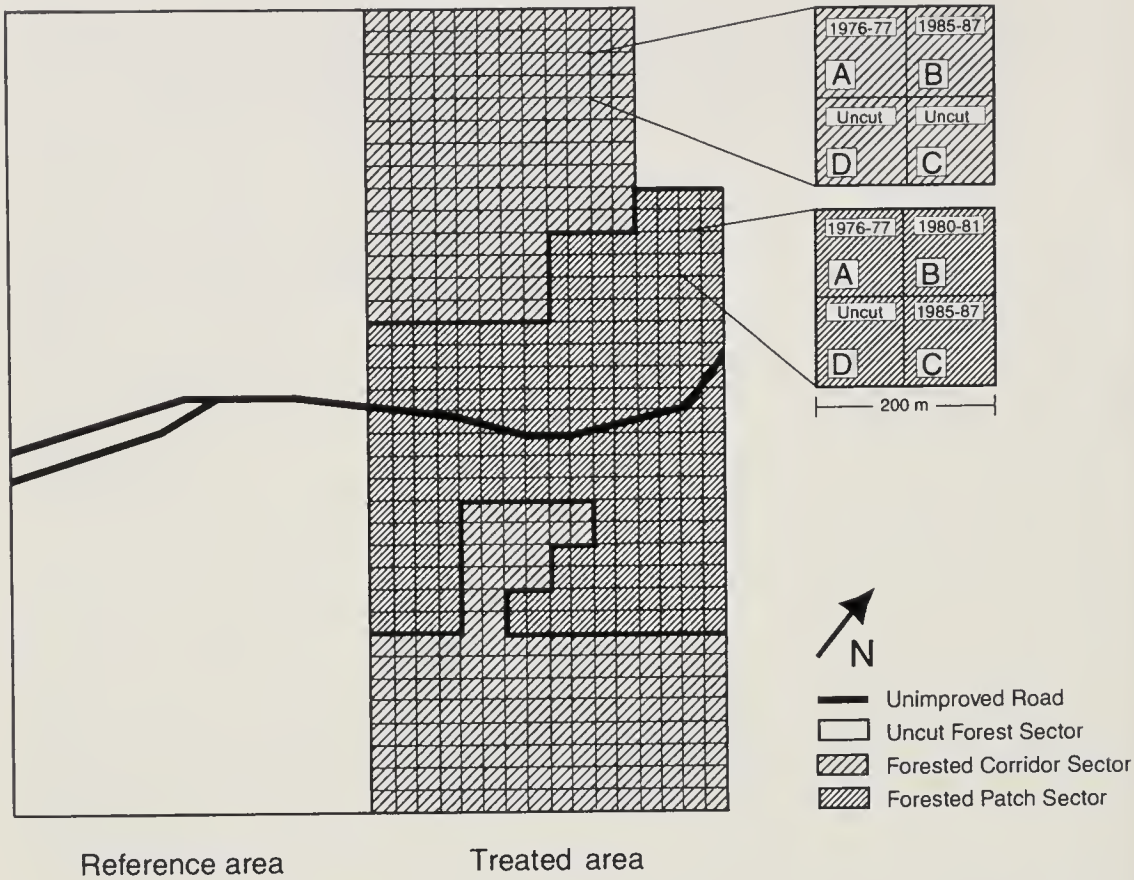

FIG. 1. Reference (contiguous forest sector) and treated (forested patch and forested corridor sectors) areas of the Barrens Grouse HMA, Centre County, Pennsylvania. Dates of clearcutting cycles (1–3) are given in plots A and B in the forested corridor sector and in plots A–C of the forested patch sector. Forest was uncut in the contiguous forest sector, in plots C and D of the forested corridor sector, and in plot D of the forested patch sector (modified from Yahner and Mahan 1996).

obtained in period 2 to those obtained in 1988–90, which was one–two years after the third cycle (termed period 1, Yahner 1993).

STUDY AREA AND METHODS

I conducted the study at the 1166-ha Barrens Grouse HMA, State Game Lands 176, Centre County, Pennsylvania, from May 1993 through July 1995 (period 2, 6–8 years subsequent to the third cutting cycle). My study site contains a reference and a treated area of similar size (Fig. 1) (Yahner 1993, 1994; Yahner and Mahan 1996). The reference area is uncut and is termed the contiguous forest sector. The treated area is separated into a forested patch and a forested corridor sector. Forest in the contiguous forest sector, in uncut plots of both forested patch and corridor sectors, and surrounding the Barrens Grouse HMA has not been cut for approximately 75–80 years.

Major overstory trees (woody stem > 7.5 cm dbh and > 1.5 m tall) on the three sectors were quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), red maple (*Acer rubrum*), and pitch pine (*Pinus rigida*). Major understory trees

TABLE 1

SPECIES RICHNESS (*S*) AND ABUNDANCE (*N*, NO./10 HA) OF ALL SPECIES COMBINED AND OF TWO MAJOR FORAGING GUILDS IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1993–94 AND 1994–95 COMBINED (PERIOD 2)

	Sector			
	Contiguous forest	Forested corridor	Forested patch	Total
Species richness, *S*:				
All species combined	4	10	8	12
Trunk-bark foragers	3	7	5	8
Ground-shrub foragers	1	3	3	4
Abundance, *N*:				
All species combined	14.1	21.2	19.5	19.7
Trunk-bark foragers	7.1	18.1	15.5	15.7
Ground-shrub foragers	7.1	3.1	4.0	4.0

(woody stem = 2.5–7.5 cm dbh and > 1.5 m tall) and tall shrubs (woody stems < 2.5 cm dbh and > 1.5 m tall) were aspen, red maple, black cherry (*Prunus serotina*), and oak (Yahner 1993).

The treated area consists of 136 contiguous 4-ha blocks, with each block subdivided into four 1-ha (100- × 100-m) plots arranged in a clockwise pattern (plots A–D) (Fig. 1) (Yahner 1993, Yahner and Mahan 1996). In the forested patch sector, plot A was clearcut in winter 1976–77, plot B in winter 1980–81, and plot C in winters 1985–86 and 1986–87; this resulted in uncut forested patches (plot D) surrounded by three clearcut plots (A–C) of different ages. In the forested corridor sector, plot A was clearcut in winter 1976–77, and plot B was cut in winters 1985–86 and 1986–87. In each plot B of this sector, 15–20 overstory trees/ha were retained (Yahner 1995). This created 100-m wide corridors of uncut forest (plots C–D) adjacent to clearcut plots of two ages (plots A–B); uncut plots C and D were considered distinct from each other because proximal clearcut plots differed in age and because vegetative density near ground level was greater ($P < 0.05$) in older than in younger clearcut plots (Yahner et al. 1989). Therefore, based on age since cutting and sector, I classified the Barrens Grouse HMA into nine plot types: uncut plots in the contiguous forest sector and four plot types each (plots A–D) in forested patch and corridor sectors, respectively (after Yahner 1993).

I sampled bird communities at the same 90 1-ha plots randomly selected in a previous study (i.e., period 1) of wintering and breeding bird communities at the Barrens Grouse HMA (Yahner 1993). Of the 90 plots, 10 were in the contiguous forest sector, and 10 plots each consisted of the four habitats (plots A–D) in both forested patch and corridor sectors. Plots were representative of plots on each sector, and plot centers were located at least 50 m from disturbances, e.g., logging road, to minimize edge effects (Strelke and Dickson 1980, Yahner 1987). The minimum distance between plots was 200 m (DeSante 1986, Yahner 1993).

I visited each plot once from late December to early February during two consecutive winters (1993–1994 and 1994–95) and again in late May to late June during three consecutive breeding seasons (1993–1995). The randomized order and number of visits to plots

were identical to those used in period 1 at the Barrens Grouse HMA (Yahner 1993). Visits were made between sunrise and 10:30 hr DST. After an initial 1-min equilibrium period, I noted all birds seen or heard within a 30-m radius of the center of the plot during the subsequent 5 min (DeSante 1986, Yahner 1993). I chose a 30-m radius in order to minimize edge effects at interfaces of plots in forested patch and corridor sectors (after Repenning and Labisky 1985, Yahner 1993). Birds flying through or above the canopy were not counted.

I computed two measures of avian community structure, species richness (*S*) and population abundance (*N*), for each sector and plot type based on data obtained during winters or breeding seasons combined during period 2 (Yahner 1993). Species richness (*S*) was the number of all species combined or per foraging guild; *N* was the number of contacts (no./10 ha) of all species combined, or foraging guild or individual species. The three principal guilds were trunk-bark foragers (species typically foraging on tree trunks or large branches), ground-shrub foragers (species typically foraging on or < 2 m above ground level), and sallier-canopy foragers (species typically foraging > 2 m above ground level in vegetation) (Yahner 1986, 1993).

I also derived an importance value (*IV*) for each species per season (winters or breeding seasons combined) as a means of comparing the importance of a given species in period 2 to the total bird community (Yahner 1993). An *IV* was the sum of a relative numerical component (*RN*) and a relative distribution component (*RD*). *RN* was the abundance (total number of contacts) of a given species at the 90 plots pooled from the two winters or the three breeding seasons and divided by the abundance recorded for the most abundant species. Maximum abundance was 32 contacts for Black-capped Chickadees (scientific names are given in Tables 2 and 4) in winter and 110 contacts for Ovenbirds in the breeding season (×100). *RD* was the proportion of the nine plot types in which a given species was observed during winters or breeding seasons combined (×100). I summed *RN* and *RD* (max. = 200) to classify a species as being of high (*IV* ≥ 125), moderate (50–124), or low importance (≤49) in winter or the breeding season.

I compared observed versus expected numbers of contacts of all species combined, of each foraging guild, and of each species among the three sectors in period 2, using *G*-tests for goodness-of-fit (Sokal and Rohlf 1995, after Yahner 1993). If observed versus expected numbers of a given bird variable differed among sectors, I then used *a posteriori* *G*-tests for goodness-of-fit about the cell (i.e., sector) of interest. Observed versus expected numbers of contacts were also examined among plots within forested corridor and patch sectors if sample sizes were adequate to meet assumptions of the test. Expected numbers of contacts were obtained by multiplying the number of contacts of all species combined, guild, or individual species by the proportion of total number of plots per sector or plot type.

In addition, I compared observed versus expected numbers of contacts of all species combined, each foraging guild, and each species in a given sector or plot type immediately after the third cycle (period 1) (Yahner 1993, 1994) to numbers found in the present study (period 2) using *G*-tests for goodness-of-fit. Expected numbers of contacts were obtained by summing the total number of contacts obtained in a given sector or plot type in both periods 1 and 2 and dividing by 2. In all analyses, data were pooled by seasons (winter or breeding) to give a better measure of habitat-use patterns within and between periods and to increase sample size for statistical analyses (after Rice et al. 1984; Yahner 1986, 1993).

RESULTS

Spatial differences among sectors in winter (Period 2).—I observed 12 bird species in winters 1993–94 and 1994–95 combined at the Barrens Grouse HMA (Table 1). Most species (67%) were trunk-bark foragers,

TABLE 2

ABUNDANCE (*N*, NO./10 HA) OF INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AND IMPORTANCE COMPONENTS (*IV, RN, RD*) OF INDIVIDUAL SPECIES IN THREE SECTORS POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1993–94 AND 1994–95 COMBINED (PERIOD 2)

	Sector				
Classification: Species[a]	Contiguous forest	Forested corridor	Forested patch	Total	*IV (RN, RD)*[b]
High importance:					
Black-capped Chickadee (*Parus atricapillus*)[c]	0.0[d]	5.7	8.4	6.3	144 (100, 44)
Moderate importance:					
Tufted Titmouse (*Parus bicolor*)	8.8	3.5	0.9	2.9	91 (47, 44)
Blue Jay (*Cyanocitta cristata*)	5.3	1.8	1.8	2.2	90 (34, 56)
Ruffed Grouse (*Bonasa umbellus*)	7.1	0.9	0.0	1.2	75 (19, 56)
Golden-crowned Kinglet (*Regulus satrapa*)	12.4	0.9	0.0	1.8	72 (28, 44)
White-breasted Nuthatch (*Sitta carolinensis*)	5.3	3.5	0.4	2.4	82 (38, 44)
Low importance:					
Downy Woodpecker (*Picoides pubescens*)	1.8	1.8	0.0	1.0	38 (16, 22)
Hairy Woodpecker (*P. villosus*)	0.0	2.2	0.0	1.0	38 (16, 22)
Northern Cardinal (*Cardinalis cardinalis*)	0.0	0.4	0.0	0.2	14 (3, 11)
Pileated Woodpecker (*Dryocopus pileatus*)	0.0	0.4	0.0	0.2	14 (3, 11)
Eastern Wild Turkey (*Meleagris gallopavo*)	3.5	0.0	0.0	0.4	17 (6, 11)
Red-bellied Woodpecker (*Centurus carolinus*)	0.0	0.0	0.4	0.2	14 (3, 11)

[a] Classification of bird species was based arbitrarily on *IV* values: high importance, $IV \geq 125$; moderate importance, $IV = 50–124$; low importance, $IV \leq 49$.

[b] Importance components: $IV = RN + RD$, where RN = the relative numerical component and RD = the relative distribution component.

[c] Observed versus expected number of contacts varied significantly among sectors; $G \geq 5.99$, df = 2, $P \leq 0.05$; *G*-test for goodness-of-fit.

[d] Observed number of contacts in this sector was significantly less than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$, *G*-test for goodness-of-fit.

and *N* of trunk-bark foragers was nearly four-fold that of ground-shrub foragers (15.7 vs 4.0 individuals/10 ha, respectively). More species (S = 10) were noted in the forested corridor sector than in either the contiguous forest sector (S = 4) or the forested patch sector (S = 8). In addition, *N* of all species combined was higher in the forested corridor sector (21.2 individuals/10 ha) than in the other sectors (contiguous forest = 14.1 individuals/10 ha, forested patch = 19.5 individuals/ha).

The Black-capped Chickadee was the most common wintering species and was the only species classified as being of high importance ($IV \geq 125$) to the wintering bird community (Table 2). Abundance of chickadees varied among sectors, with fewer contacts in the contiguous forest com-

pared to either forested corridor or patch sectors. Five species in decreasing order of abundance and of moderate importance (IV = 50–124) were Tufted Titmice, White-breasted Nuthatches, Blue Jays, Golden-crowned Kinglets, and Ruffed Grouse; although not significant ($P > 0.05$), abundances of each of these five species tended to be higher in the contiguous forest sector than in the other two sectors.

Spatial differences among plot types in winter (period 2).—Use of the four plot types by all species combined was significantly different in the forested corridor sector ($G = 25.5$, df = 3, $P < 0.005$). Clearcut plot types (plots A and B) were used less than expected ($G = 9.3$, df = 1, $P < 0.001$), whereas an uncut type (plot C) was used more than expected ($G = 13.0$, df = 1, $P < 0.005$). Abundance of trunk-bark foragers differed among plot types ($G = 36.7$, df = 3, $P < 0.005$), with significantly fewer contacts in recent clearcut plots (plots A and B) ($G \geq 12.0$, df = 1, $P < 0.005$) versus more contacts in uncut plots (plots C and D) ($G \geq 3.9$, df = 1, $P < 0.05$).

Use of plot types by all species combined also varied significantly in the forested patch sector ($G = 58.9$, df = 3, $P < 0.005$). The most recent clearcut plot (plot C) was used less than expected, but the uncut plot (plot D) was used more than expected ($G \geq 18.8$, df = 1, $P < 0.005$).

Spatial differences among sectors in the breeding season (period 2).—I recorded 40 species during the three breeding seasons combined (1993–95) at the Barrens Grouse HMA (Table 3). Compared to winter, most breeding species (S = 21, 53%) were ground-bark foragers; the remaining species were sallier-canopy (S = 12, 30%) and trunk-bark foragers (S = 7, 17%). Nearly all breeding species (S = 37) were noted in the forested corridor sector compared to fewer in forested patch (S = 32) and contiguous forest (S = 15) sectors. Ground-shrub foraging species occurred principally in the forested corridor and patch sectors (S = 20 and 18, respectively), with few in the contiguous forest sector (S = 3); conversely, S of both trunk-bark and sallier-canopy guilds was relatively similar among sectors (S = 4–5 and 7–10, respectively).

Abundance of all species combined tended to be lower ($0.10 > P > 0.05$) in the contiguous forest sector than in other sectors (Table 3). Abundance of ground-shrub foragers was significantly less than expected in the contiguous forest sector and greater than expected in the forested patch sector. Conversely, N of sallier-canopy foragers was higher than expected in contiguous forest and forested corridor sectors but lower in the forested patch sector.

Five (13%) of the 40 breeding species were categorized as being highly important to the breeding bird community, including Ovenbirds, Eastern Towhees, Common Yellowthroats, Red-eyed Vireos, and Rose-breasted

TABLE 3

SPECIES RICHNESS (*S*) AND ABUNDANCE (*N*, NO./10 HA) OF ALL SPECIES COMBINED AND OF THREE MAJOR FORAGING GUILDS IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING BREEDING SEASONS 1993–95 COMBINED (PERIOD 2)

	Sector			
	Contiguous forest	Forested corridor	Forested patch	Total
Species richness, *S*:				
All species combined	15	37	32	40
Trunk-bark foragers	4	6	5	7
Ground-shrub foragers	3	20	19	21
Sallier-canopy foragers	8	11	8	12
Abundance, *N*:				
All species combined	74.3	95.5	97.3	93.9
Trunk-bark foragers	7.1	8.0	10.3	8.9
Ground-shrub foragers[a]	24.8[b]	57.5	76.4[c]	62.2
Sallier-canopy foragers[a]	42.4[c]	30.0[c]	10.6[c]	22.8

[a] Observed versus expected number of contacts varied significantly among sectors; $G \geq 5.99$, df = 2, $P \leq 0.05$; *G*-test for goodness-of-fit.

[b] Observed number of contacts in this sector was significantly greater than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

[c] Observed number of contacts in this sector was significantly less than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

Grosbeaks (Table 4). Fourteen (35%) and 21 (52%) species were of moderate or low importance, respectively. Eleven (28%) breeding species varied significantly among the three sectors. For instance, abundance of Red-eyed Vireos was significantly higher than expected in the contiguous forest sector versus lower in the forested patch sector. Furthermore, some less common species, including Eastern Wood-Pewees, Downy Woodpeckers, Blue-gray Gnatcatchers, and Least Flycatchers tended to be more abundant in the contiguous forest than in either the forested corridor or the forested patch sector. Brown-headed Cowbirds, American Redstarts, and Baltimore Orioles predominated in the forested corridor sector. In contrast, abundances of size ground-shrub foragers, including Ovenbirds, Eastern Towhees, Common Yellowthroats, Gray Catbirds, Black-and-white Warblers, and Golden-winged Warblers, were most common in the forested patch sector.

Spatial differences among plot types in the breeding season (period 2).—Abundances of all species combined and of ground-shrub foragers differed among plot types in the forested corridor sector ($G \geq = 79.6$, df = 3, $P < 0.005$), with the most recent clearcut plot (plot B) used more than expected and the other three plot types used less than expected (*G*

TABLE 4

ABUNDANCE (*N*, NO./10 HA) OF INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AND IMPORTANCE COMPONENTS (*IV, RN, RD*) OF INDIVIDUAL SPECIES IN THREE SECTORS POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING BREEDING SEASONS 1993–95 COMBINED (PERIOD 2)

Classification: Species[a]	Sector			Total	*IV (RN, RD)*[b]
	Contiguous forest	Forested corridor	Forested patch		
High importance:					
Ovenbird (*Seiurus aurocapillus*)[d]	17.7	10.0[e]	18.0[f]	14.4	200 (100, 100)
Eastern Towhee (*Pipilo erythrophthalmus*)[d]	0.0[e]	8.8	15.0[f]	10.6	163 (74, 89)
Common Yellowthroat (*Geothylpis trichas*)[d]	0.0[e]	9.1	9.4[f]	8.3	135 (57, 78)
Red-eyed Vireo (*Vireo olivaceus*)[d]	17.7[f]	6.0	4.4[e]	6.6	134 (45, 89)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	4.7	6.5	3.2	4.8	134 (34, 100)
Moderate importance:					
Gray Catbird (*Dumetella carolinensis*)[d]	0.0[e]	7.8	10.0[f]	7.9	122 (55, 67)
Chestnut-sided Warbler (*Dendroica pensylvanica*)[d]	0.0[e]	5.0	6.2	5.0	90 (34, 56)
Black-and-white Warbler (*Mniotilta varia*)[d]	0.0	2.4	5.6[f]	3.5	103 (25, 78)
Golden-winged Warbler (*Vermivora chrystoptera*)[d]	0.0	0.3[e]	6.8[f]	3.1	67 (23, 44)
Brown-headed Cowbird (*Molothrus ater*)[d]	5.9	5.3[f]	0.3[e]	3.1	90 (23, 67)
American Redstart (*Setophaga ruticilla*)[d]	3.5	5.3[f]	0.0[e]	2.8	75 (19, 56)
Field Sparrow (*Spizella pusilla*)	0.0	2.4	3.2	2.5	61 (17, 44)
Black-capped Chickadee (*Parus atricapillus*)	1.2	2.9	2.1	2.4	105 (16, 89)
Tufted Titmouse (*P. bicolor*)	2.4	1.5	1.5	1.6	78 (11, 67)
Wood Thrush (*Hylocichla mustelina*)	0.0	2.4	1.2	1.6	67 (11, 56)
Baltimore Oriole (*Icterus galbula*)[d]	0.0	5.0[f]	0.0[e]	2.2	48 (15, 33)
Eastern Wood-Pewee (*Contopus virens*)	7.1	2.4	0.0	1.8	46 (13, 33)

TABLE 4
CONTINUED

Classification: Species[a]	Sector			Total	*IV* (*RN*, *RD*)[b]
	Contiguous forest	Forested corridor	Forested patch		
Downy Woodpecker (*Picoides pubescens*)	2.4	0.3	0.9	0.8	38 (5, 33)
Blue-gray Gnatcatcher (*Polioptila caerulea*)	2.4	0.9	0.3	0.8	49 (5, 44)
Indigo Bunting (*Passeria cyanea*)	0.0	0.6	1.2	0.8	38 (5, 33)
Least Flycatcher (*Empidonax minimus*)	3.5	0.0	0.3	0.5	26 (4, 22)
Ruffed Grouse (*Bonasa umbellus*)	0.0	0.6	0.6	0.5	48 (4, 44)
Cedar Waxwing (*Bombycilla cedrorum*)	0.0	1.2	0.0	0.5	15 (4, 11)
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.0	0.3	0.6	0.4	36 (3, 33)
Nashville Warbler (*Vermivora ruficapilla*)	0.0	0.3	0.6	0.4	36 (3, 33)
Worm-eating Warbler (*Helmitheros vermivorus*)	0.0	0.3	0.6	0.4	36 (3, 33)
Chipping Sparrow (*Spizella passerina*)	0.0	0.3	0.03	0.3	24 (2, 22)
White-breasted Nuthatch (*Sitta carlinensis*)	0.0	0.6	0.0	0.3	13 (2, 11)
Pine Warbler (*Dendroica pinus*)	0.0	0.3	0.3	0.3	24 (2, 22)
Common Grackle (*Quiscalus quiscula*)	0.0	0.3	0.3	0.3	24 (2, 22)
Brown Thrasher (*Toxostoma rufum*)	0.0	0.0	0.6	0.3	13 (2, 11)
American Crow (*Corvus brachyrhynchos*)	0.0	0.3	0.3	0.3	13 (2, 11)
American Goldfinch (*Carduelis tristis*)	0.0	0.3	0.3	0.3	24 (2, 22)
Hairy Woodpecker (*Picoides villosus*)	1.2	0.3	0.0	0.3	24 (2, 22)
Yellow-throated Vireo (*Vireo flavifrons*)	0.0	0.3	0.0	0.1	12 (1, 11)
Red-bellied Woodpecker (*Centurus carolinus*)	0.0	0.0	0.3	0.1	12 (1, 11)

[a] Classification of bird species was based arbitrarily on *IV* values: high importance, $IV \geq 125$; moderate importance, $IV = 50–124$; low importance, $IV \leq 49$.
[b] Importance components: $IV = RN + RD$, where RN = the relative numerical component and RD = the relative distribution component.
[c] Observed versus expected number of contacts varied significantly among sectors; $G \geq 5.99$, df = 2, $P \leq 0.05$; *G*-test for goodness-of-fit.
[d] Observed number of contacts in this sector was significantly greater than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.
[e] Observed number of contacts in this sector was significantly less than expected; $G \geq 3.81$, df = 1, $P \leq 0.05$; *G*-test for goodness-of-fit.

TABLE 5

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2). ONLY GUILDS OR INDIVIDUAL SPECIES WITH A SIGNIFICANT CHANGE IN ONE OR MORE SECTORS AND WITH >10 TOTAL CONTACTS IN A GIVEN SECTOR ARE PRESENTED

	Sector			
Classification:	Contiguous forest	Forested corridor	Forested patch	Total
Species richness	0.0	0.0	+14.3	+9.0
Abundance				
All species combined		+9.0	+51.7	+23.5
Trunk-bark foragers		+32.3	+66.7	+37.9[a]
Tufted Titmouse				+225.0[a]
White-breasted Nuthatch				+200.0[a]
Blue Jay				+266.7[a]

[a] Observed abundance was significantly different from expected during winters 1988–89 and 1989–90 combined versus winters 1993–94 and 1994–95 combined; $G \geq 3.81$, df = 1, $P < 0.05$. G-test for goodness-of-fit.

≥ 4.1, df = 1, $P < 0.05$). Use of plot types by towhees, yellowthroats, and catbirds also varied in the forested corridor sector ($G \geq 14.2$, df = 3, $P < 0.001$). Abundances of each of these three species were greater than expected in plot B but less than expected in plot C ($G \geq 4.3$, df = 1, $P < 0.05$).

Abundances of all species combined, of ground-shrub foragers, and of sallier-canopy foragers differed among plot types in the forested patch sector ($G \geq = 13.1$, df = 3, $P < 0.005$). Older plots (plots A and D) were used less than expected, and the most recent clearcut plots (plot C) were used more than expected by all species combined and by ground-shrub foragers ($G \geq 4.1$, df = 1, $P < 0.05$). In contrast, sallier-canopy foragers used the two most recent clearcut plots (plots B and C) less than expected but used the uncut plots (plot D) more than expected ($G \geq 4.4$, df = 1, $P < 0.05$). Some examples of differential use of plot types by individual species in the forested patch sector were less than expected use of plot C by Ovenbirds versus greater than expected use of plot C by catbirds, Chestnut-sided Warblers, and Golden-winged Warblers ($G \geq 6.2$, df = 1, $P < 0.005$).

Temporal trends in winter (periods 1 vs 2).—Species richness increased slightly (9.0% increase) from period 1 to period 2 at the Barrens Grouse HMA, with a change observed only in the forest patch sector (Table 5). However, abundances of trunk-bark foragers increased nearly 38% from

TABLE 6

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN FOUR PLOT TYPES EACH OF THE FORESTED CORRIDOR AND PATCH SECTORS AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2)[a]

Sector	Type			
	Plot A	Plot B	Plot C	Plot D
Forested corridor:				
Species richness	−50.0	−33.3	+75.0	−42.9
Abundance				
All species combined	−66.7[a]		+420.0[a]	−36.0
Forested patch:				
Species richness	0.0	+33.3	−50.0	+40.0
Abundance				
All species combined	−50.0	+175.0		+216.7[b]
Trunk-bark foragers		+266.7[b]	+340.0[b]	+91.7
Black-capped Chickadee		+900.0[a]		+50.0

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.

[b] Observed number of contacts was significantly different from expected in winters 1988–89 and 1989–90 combined versus winters 1993–94 and 1994–95 combined; $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

period 1 to period 2; in addition, *N* of Tufted Titmice, White-breasted Nuthatches, and Blue Jays increased at least 200% from period 1 to 2.

In the forested corridor sector, richness and abundances of all species combined increased from period 1 to period 2 in plot C but not in the other three plot types (Table 6). Also, *N* of all species combined declined significantly in the oldest clearcut plots (plot A). In the forested patch sector, *S* increased in two plot types (plots B and D) but decreased in the most recent clearcut plots (plot C) from period 1 to period 2. Moreover, *N* of all species in uncut types (plot D), of trunk-bark foragers in the two most recent clearcut types (plots B and C), and of Black-capped Chickadees in plot B increased between periods in the forested patch sector.

Temporal trends in the breeding season (periods 1 vs 2).—As in winter, *S* in the breeding season increased slightly (+5.3%) from periods 1 to 2, especially in both forested corridor and patch sectors (Table 7). Abundances of all species combined, of sallier-canopy foragers, and of five species (e.g., Ovenbirds) at the Barrens Grouse HMA increased significantly from period 1 to 2, whereas *N* of Common Yellowthroats, Scarlet Tanagers, and Indigo Buntings declined significantly between periods. In the forested corridor sector, *N* of Ovenbirds, Red-eyed Vireos, and Brown-

TABLE 7

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN THREE SECTORS OF FOREST MANAGEMENT AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM WINTERS 1988–90 (PERIOD 1) TO WINTERS 1993–95 (PERIOD 2)[a]

	Sector			
Classification:	Contiguous forest	Forested corridor	Forested patch	Total
Species richness	+14.2	+19.3	−12.5	+5.3
Abundance				
All species combined	+8.6	+37.3[b]	+4.1	+17.3[b]
Ground-shrub foragers	+16.7	+30.0[b]	+0.8	+11.8
Sallier-canopy foragers	+20.0	+75.9[b]	+2.9	+40.3[b]
Ovenbird	+36.4	+325.0[b]	+144.0[b]	+150.0[b]
Common Yellowthroat		0.0	−44.8[b]	−29.2[b]
Red-eyed Vireo	+36.4	+122.2[b]	+25.0	+56.3[b]
Rose-breasted Grosbeak		+83.3	+37.5	+85.0[b]
Black-and-white Warbler		+166.7	+137.5[a]	+125.0[b]
Brown-headed Cowbird		+260.0[b]		+118.2[b]
Field Sparrow			−56.0[a]	−42.4
Scarlet Tanager		−36.4	−57.1	−54.2[b]
Indigo Bunting	−50.0	−81.8		−216.7[b]

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.

[b] Observed number of contacts was significantly different from expected in breeding seasons 1988–90 combined versus breeding seasons 1993–95 combined; $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

headed Cowbirds increased significantly between periods; in the forested patch sector, *N* of Black-and-white Warblers increased while those of Common Yellowthroats and Field Sparrows decreased.

In the forested corridor sector, *S* showed the greatest change in the most recent clearcut plots (plot B, +28.6%) from period 1 to 2 (Table 8). Similarly, I found significant increases in *N* of all species combined, ground-shrub foragers, sallier-canopy foragers, Gray Catbirds, Chestnut-sided Warblers, and cowbirds in plot B between periods. In contrast, abundance of Ovenbirds increased but that of ground-shrub foragers in general declined in the oldest clearcut plots (plot A).

In the forested patch sector, *S* increased primarily in the two most recent types of clearcut plots (plots B and C) from period 1 to 2 (Table 8). I observed significant increases in *N* between periods with all species combined, ground-shrub foragers, catbirds, and Golden-winged Warblers in plot C and with Ovenbirds in the two older clearcut plots (plots A and B). Conversely, *N* of ground-shrub foragers and catbirds declined in the oldest clearcut plot (plot A) while that of yellowthroats decreased in plot B.

TABLE 8

PERCENT CHANGE (+ OR −) IN SPECIES RICHNESS AND ABUNDANCE OF ALL SPECIES COMBINED, FORAGING GUILDS, AND INDIVIDUAL SPECIES IN FOUR PLOT TYPES EACH OF THE FORESTED CORRIDOR AND PATCH SECTORS AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, FROM BREEDING SEASONS 1988–90 (PERIOD 1) TO BREEDING SEASONS 1993–95 (PERIOD 2)[a]

Sector	Type			
	Plot A	Plot B	Plot C	Plot D
Forested corridor:				
Species richness	+5.3	+28.6	−19.0	+17.6
Abundance				
All species combined	−21.5	+113.8[b]	−10.0	+100.0[b]
Ground-shrub foragers	−35.7[b]	+88.1[b]	−8.0	+133.3[b]
Sallier-canopy foragers	+20.0	+218.2[b]	+14.3	+73.3
Ovenbird	+233.3[b]	+166.7		+550.0[b]
Gray Catbird		+300.0[b]		
Chestnut-sided Warbler		+275.0[b]		
Brown-headed Cowbird		+400.0[b]		
Forested patch:				
Species richness	0.0	+42.9	+45.5	+5.9
Abundance				
All species combined	−22.4	−13.3	+59.0[b]	−17.1
Ground-shrub foragers	−31.4[b]	−18.5	+48.3[b]	−18.4
Sallier-canopy foragers				
Ovenbird	+120.0[b]	+750.0[b]		+46.2
Common Yellowthroat	−55.6	−83.9[b]	+29.4	
Gray Catbird	−81.3[b]	+8.3	+1700.0[a]	
Golden-winged Warbler		−25.0	+200.0[a]	

[a] Only guilds or individual species with a significant change in one or more sectors and with >10 total contacts in a given sector are presented.

[b] Observed number of contacts was significantly different from expected in breeding seasons 1988–90 combined versus breeding seasons 1993–95 combined; $G \geq 3.81$, df = 1, $P \leq 0.05$; G-test for goodness-of-fit.

DISCUSSION

Wintering bird community dynamics.—I noted at least five trends in the community structure of wintering birds on my study site in central Pennsylvania from 1988–95. First, abundances of all species combined and of the two foraging guilds (trunk-bark and ground-shrub foragers) did not differ among sectors (contiguous forest, forested corridor, and forested patch) for nearly a decade after the third cutting cycle (Yahner 1993, present study). This supports the contention that species richness and population abundances of wintering birds are generally less affected by small-scale forest clearcutting than breeding birds (Yahner 1985, Maurer and Heywood 1993).

A second trend was the continued high abundance of wintering trunk-bark foragers relative to ground-bark foragers at the Barrens Grouse HMA (e.g., Yahner 1993), which may be related to the availability of foraging substrate for these guilds in winter. Rough-barked trees (e.g., *Quercus*) were common in uncut plot types throughout the study site (Yahner 1987). These types of trees are important as foraging substrate because of numerous crevices for arthropods that serve as an important food for trunk-bark foragers (Brawn et al. 1982, Morrison et al. 1985). I attribute the relative lack of wintering ground-shrub foragers to a paucity of weed seeds as a food resource (Yahner 1986, 1993). Weedy, herbaceous vegetation was mainly restricted to habitat immediately adjacent to the unimproved road bisecting the study site (Fig. 1). In contrast, ground-shrub foragers, e.g., White-throated Sparrows (*Zonotrichia albicollis*), were quite common in winter at nearby (<10 km) irrigated forested stands where herbaceous vegetation was abundant (Rollfinke and Yahner 1990).

A third trend in the wintering bird community was greater use of older plots (e.g., plot C in the forested corridor sector) and lesser use of more recent clearcut plots (e.g., plot C in the forested patch sector) subsequent to both second and third cutting cycles (Yahner 1987, 1993; present study). Interiors of uncut plots likely provided a better microclimate for wintering birds (Ranney et al. 1981) and, therefore, reduced the energetic costs associated with foraging (Morrison et al. 1986, Yahner 1987).

A fourth trend in winter at the Barrens Grouse HMA was the common occurrence of Black-capped Chickadees in both periods (Yahner 1986, 1993; present study). This species is very common in managed stands throughout the eastern deciduous forests during winter (e.g., Conner et al. 1979, Rollfinke and Yahner 1990). Moreover, perhaps chickadees were particularly abundant in the intermediate-aged clearcut plot (plot B) in the forested patch sector during period 2 because of plant succession; for example, the density of understory stems in plot B of this sector increased 71% from period 1 to 2 (Yahner, unpubl. data). In winter, Black-capped Chickadees prefer to forage on small woody stems in the understory (Brawn et al. 1982, Morrison et al. 1985).

A final trend in the wintering bird community were greater abundances of three species (titmice, nuthatches, and jays) in period 2 than in period 1, which may also be partially explained by plant succession and regional population increases. The density of overstory trees in clearcut plot types in forested corridor and patch sectors combined increased 79% from periods 1 to 2 (Yahner, unpubl. data), thereby providing more foraging substrate for trunk-bark foragers, such as titmice and nuthatches. Although mast production was not measured in my study, a greater density of overstory trees between periods probably increased mast availability, which

is an important winter food resource for Blue Jays (Smith 1986). Furthermore, each of these three species has shown a general population increase in central Pennsylvania (e.g., Allegheny Plateau) over the past few decades (Wiedenfeld et al. 1992).

Breeding bird community dynamics.—I noted six trends in the community structure of breeding birds on the managed forested landscape in central Pennsylvania. First, richness of all species combined tended to be much higher on both forested corridor and patch sectors than on the contiguous forest sector; a higher *S* on managed versus reference (uncut) forested landscapes is also reported on this study site prior to period 2 (Yahner 1986, 1993) and in other studies of breeding bird communities (e.g., Welsh and Healy 1993). However, I caution that a lower *S* on the contiguous forest sector may be attributed in part to a reduced sampling effort on the reference than on the treated area of the Barrens Grouse HMA (see Conner and McCoy 1979).

Second, although abundance of all species combined did not vary among the three sectors for several years since the third cutting cycle at the Barrens Grouse HMA, abundances of the two major guilds, i.e., ground-shrub and sallier-canopy foragers, differed among sectors as a probable consequence of forest management (Yahner 1993; present study). Ground-shrub foragers, which represented the principal guild in both periods, were most common in the forested patch sector because of the creation of considerable amounts of edge and brushy habitat via clearcutting. Conversely, sallier-canopy foragers occurred mainly in the other two sectors (contiguous forest and forested corridor) in period 2 because of abundant overstory trees as foraging substrate (e.g., Yahner 1987); furthermore, recent clearcut plots (plot B) in the corridor sector were used extensively by sallier-canopy foragers in possible response to the retention of residual trees (Yahner 1995).

Third, in terms of population abundances, five ground-shrub foraging species in period 2 were positively affected by forest clearcutting; these included towhees, catbirds, yellowthroats, Black-and-white Warblers, and Golden-winged Warblers. A similar response by these species to clearcutting has been noted in other studies (e.g., Crawford et al. 1981; Yahner 1986, 1993; Thompson et al. 1992). These species were found mainly in the most recent clearcut plots which contained dense, brushy vegetation near ground level compared to uncut plots at the Barrens Grouse HMA (Yahner, unpubl. data). The towhee is an example of a brush-inhabiting species whose populations are doing quite well at the Barrens Grouse HMA (Lewis 1996) but have shown declines in recent years as a plausible result of forest maturation throughout much of the Northeast (e.g., Hagan 1993). Common Yellowthroats and Golden-winged Warblers also have

exhibited population declines over the past few decades in eastern North America (James et al. 1996). My findings, therefore, confirm the importance of disturbed habitats, such as small clearcut plots, to long-term trends in populations of early-successional species (DeGraaf et al. 1993, Litvaitis 1993, Yahner 1995). In addition, nesting success of species for which data from the Barrens Grouse HMA are available (e.g., catbirds, towhees, yellowthroats, and Wood Thrushes) is comparable to those reported in other modified landscapes (see Yahner 1991, Yahner and Ross 1996).

A fourth trend in the breeding bird community at the Barrens Grouse HMA was the recent increase in abundance of the Ovenbird since period 1, whereas the Eastern Towhee was the predominant breeding species prior to period 2 (Yahner 1986, 1993). The Ovenbird was particularly common in the uncut plots of the highly fragmented forest patch sector, suggesting that Ovenbird populations on a localized basis may be unaffected by small-scale forest clearcutting (see Thompson et al. 1992, Yahner 1993). Some studies in more intensively fragmented landscapes, however, have contended that Ovenbirds are area-dependent and, hence, negatively affected by habitat fragmentation (e.g., Robbins et al. 1989). I have no data to confirm whether Ovenbirds using small (1-ha) plots in the forested patch sector had reduced reproductive success (e.g., Gibbs and Faaborg 1990, Donovan et al. 1995), although the frequency of paired Ovenbirds that were presumed to be mated did not vary ($P > 0.10$) among the three sectors at the Barrens Grouse HMA (Yahner, unpubl. data). On the other hand, Red-eyed Vireos and cowbirds were perhaps the only breeding species negatively affected by forest clearcutting. Abundance of vireos was higher in the contiguous forest sector than in other sectors during period 2. Other studies (e.g., Robbins et al. 1989, Thompson et al. 1992) have concluded that habitat fragmentation can negatively influence abundance and distribution of Red-eyed Vireos. The cowbird was possibly negatively affected by clearcutting with higher numbers of this species observed in forested corridor and contiguous forest sectors than in the forested patch sector during period 2. But this trend is not surprising because recent evidence has suggested that rates of cowbird parasitism in the Northeast may be locally higher in forest-interior than in forest-edge habitats (Hahn and Hatfield 1995).

A fifth trend was an increase in abundances of several species (e.g., Ovenbirds, Red-eyed Vireos, Black-and-white Warblers, and Rose-breasted Grosbeaks) from period 1 to 2 at the Barrens Grouse HMA, which may be in part be a consequence of plant successional changes (see Crawford et al. 1981, Yahner 1993). Of these species, populations of Red-eyed Vireos have increased significantly on a regional scale, based on trends

confirmed by Breeding Bird Surveys in eastern North America from 1966–1991 (Peterjohn and Sauer 1994).

A sixth and opposite trend was a significant decline in population abundances of Common Yellowthroats, Scarlet Tanagers, Field Sparrows, and Indigo Buntings at the Barrens Grouse HMA from period 1 to 2. I attributed declines in yellowthroats and Field Sparrows to plant succession, whereby recent clearcut plots (e.g., plot B in the forested patch sector) in period 2 became less suitable as breeding habitat than in period 1 (see Yahner 1986, 1993). I have no explanation for declines in tanagers and buntings on my study site, but declines in Field Sparrows at the Barrens Grouse HMA may be related to significant declines in this species from 1966–91 throughout much of eastern North America (see Askins 1993).

Based on studies since the early 1980s at the Barrens Grouse HMA, I conclude the small-scale forest management has not resulted in a long-term, detrimental effect on bird communities. Forest fragmentation and subsequent plant succession, for instance, have had minimal impact on species richness of wintering and breeding bird communities in this managed forested landscape. Furthermore, abundances of bird species dependent on contiguous uncut forests were generally unaffected over the past several years, whereas abundances of early successional species were usually augmented by small-scale forest management.

Habitat management resulting in a combination of contiguous forest, corridors, and small patches, provides a variety of suitable conditions for both wintering and breeding bird communities. A managed landscape containing contiguous forest and forested strip corridors particularly benefits trunk-bark foragers in winter and sallier-canopy foragers in the breeding season. Furthermore, the retention of residual trees in clearcut plots is of value to sallier-canopy foraging species. When the landscape also contains a mosaic of small forested patches, ground-shrub foragers are positively affected in the breeding season, e.g., Eastern Towhees. However, as plant succession progresses on a managed landscape, such as that created for grouse habitat in central Pennsylvania, it likely will become less suitable for certain breeding species, such as Common Yellowthroats and Field Sparrows, that rely on recent clearcut plots. Hence, a variety of breeding bird species will occur if a continuum of plot types ranging from early successional to uncut forested plots is present in the managed forest landscape.

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WOODPECKER ABUNDANCE AND HABITAT USE IN THREE FOREST TYPES IN EASTERN TEXAS

CLIFFORD E. SHACKELFORD[1,2] AND RICHARD N. CONNER[1]

ABSTRACT.—Woodpeckers were censused in 60 fixed-radius (300 m) circular plots (divided into eight 45°-arc pie-shaped sectors) in mature forests (60–80 years-old) of three forest types (20 plots per type) in eastern Texas: bottomland hardwood forest, longleaf pine (*Pinus palustris*) savannah, and mixed pine-hardwood forest. A total of 2242 individual woodpeckers of eight species was detected in 144 h of censusing. Vegetation characteristics in plot sectors with and without woodpeckers were compared. Woodpecker presence and abundance were primarily associated with the occurrence of large snags and logs. Red-bellied Woodpeckers (*Melanerpes carolinus*) were the most abundant and widespread species, especially in areas containing more hardwoods than pines. Red-cockaded Woodpeckers (*Picoides borealis*) were the least abundant and most habitat-restricted woodpecker, occurring only in the longleaf pine savannah. Pileated Woodpeckers (*Dryocopus pileatus*) were the most evenly distributed species among the forest types, but occurred primarily in mature forests with large snags and logs. Bottomland hardwood forests were important for Northern Flickers (*Colaptes auratus*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), and Yellow-bellied Sapsuckers (*Sphyrapicus varius*) during the fall and winter, and for Downy Woodpeckers (*Picoides pubescens*) during the summer and winter. The Hairy Woodpecker (*P. villosus*) was most frequently encountered in areas of recent disturbance in the mixed pine-hardwood forests, especially in fall. Vocal imitation of a Barred Owl (*Strix varia*) increased the number of woodpecker detections by 71%. *Received 14 Jan. 1997, accepted 10 May 1997.*

Woodpeckers are generally considered to be valuable species because they eat a variety of insects considered to be harmful to forests (Steirly 1965, Dickson et al. 1979). As primary cavity excavators, they play an important role in forest ecosystems because their abandoned cavities provide shelter and nest sites for many other vertebrates (Scott et al. 1977, Conner 1978). Numerous studies have evaluated the habitat requirements of woodpeckers in a variety of forest cover types (Williams 1975; Bull and Meslow 1977; Conner 1980, 1983; Mellen 1987; Shackelford 1994; Loose and Anderson 1995). Snags (dead standing trees) are important to woodpeckers for foraging, roosting, nesting, and drumming (Conner 1978; Conner et al. 1975, 1994a). Increasing availability of snags has been shown to increase the abundance of cavity-nesting birds, especially woodpeckers (Balda 1975, Dickson et al. 1983). Therefore, an adequate supply of snags appears to be important to support large populations of woodpeckers.

[1] Wildlife Habitat and Silviculture Laboratory (Maintained in cooperation with the College of Forestry, Stephen F. Austin State University), Southern Research Station, USDA Forest Service, Nacogdoches, Texas 75962.

[2] Present address: Texas Partners In Flight, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744.

Forest management practices in most eastern Texas forests emphasize the production of wood products for human needs, sometimes at the expense of wildlife (USDA 1973, McWilliams and Lord 1988). If current and future forest management is to accommodate the needs of cavity-using wildlife, an understanding of the distribution, abundance, and habitat use of woodpeckers is essential for management decisions. We examined the habitat conditions associated with the presence and abundance of woodpeckers in a bottomland hardwood forest, a longleaf pine forest, and a mixed-pine hardwood forest in eastern Texas.

STUDY AREAS AND METHODS

Forests in eastern Texas are dominated by three native pine species and numerous species of hardwoods (McWilliams and Lord 1988). We censused woodpeckers twice a month for a twelve-month period from March 1991 to March 1992 in a mixed pine-hardwood forest and from September 1992 to September 1993 in both longleaf pine savannah and bottomland hardwood forest. The longleaf pine savannah study area consisted almost entirely of pure, longleaf pine forest and was located on the south side of the Angelina National Forest where it is managed as an open, park-like, fire-climax ecosystem for Red-cockaded Woodpeckers (*Picoides borealis*) (Conner and Rudolph 1989). The mixed pine-hardwood study area was located on the north side of the Angelina National Forest and was dominated by an overstory mix of loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines and various species of hardwood (mostly *Quercus*, *Liquidambar*, and *Nyssa*). The bottomland hardwood forest study area was located along the upper Angelina River between Nacogdoches and Angelina counties southwest of Nacogdoches, Texas. Depending on water levels, this route was surveyed either by motor boat or all-terrain vehicle. The forest along this river consisted almost entirely of a hardwood overstory and midstory (mostly *Quercus*, *Liquidambar* and *Nyssa*) with virtually no understory. A sparse ground cover comprised of leaf litter and logs was typically washed away by periodic flooding.

Fixed-radius plots (Amman and Baldwin 1960, Edwards et al. 1981, Bibby et al. 1992) were used to determine the distribution, abundance, and habitat use of the following eight species of woodpeckers within the Pineywoods vegetational zone (Gould 1969) in eastern Texas: Northern Flickers (*Colaptes auratus*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and Red-headed (*Melanerpes erythrocephalus*), Red-bellied (*M. carolinus*), Downy (*Picoides pubescens*), Hairy (*P. villosus*), Pileated (*Dryocopus pileatus*), and Red-cockaded woodpeckers. Woodpecker populations were censused in 20 circular plots (300-m radius, 28.3 ha, Fig. 1) in each of the three forest types (a total of 60 plots) along less-traveled roads and along the Angelina River. Routes within forest types were primarily placed in areas containing extensive tracts of forests and ranged in length from 35 to 45 km. As the location of plots was dependent on the presence of large tracts of unbroken mature forest, the distribution of plots along routes was occasionally interrupted by zones of fragmentation. The physical location of permanent plot centers within mature forest habitat was randomly determined. Adjacent plot boundaries were separated by at least 100 m (700 m from plot center to plot center), with adjacent plot boundary separation averaging about 1 km (1600 m from plot center to plot center).

All woodpeckers seen or heard were recorded from the center of each plot, during a 6-min period. For the first half of the censusing period, we used the 3-min unsolicited censusing method that was adopted by the Breeding Bird Survey in the 1960s and many other subsequent studies. The first 3-min period was spent tallying woodpecker detections, while

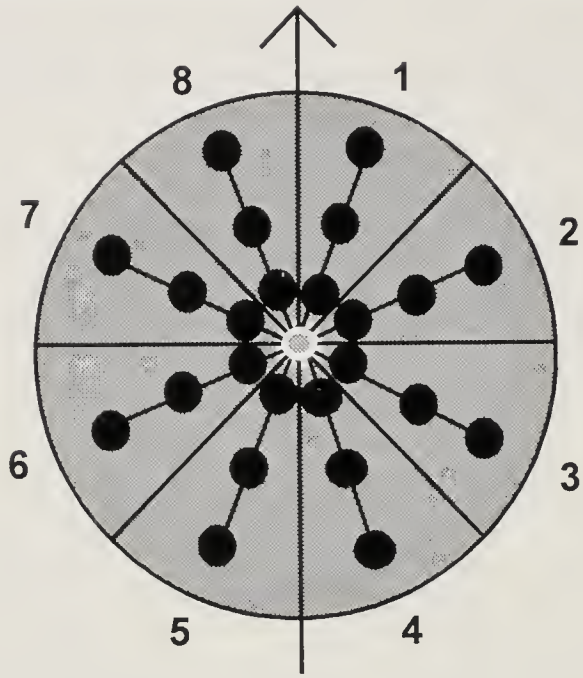

FIG. 1. Design of plots (300-m radius) used for censusing woodpeckers showing the eight 45°-arc sectors, each with a bisecting transect with three black dots indicating vegetation subplots.

the second 3-min period was spent recording woodpecker observations after the call of a Barred Owl (*Strix varia*) was vocally given by the observer for approximately 10 seconds at each minute of the 3-min period. This call technique was used to increase the probability of woodpecker detections, since we knew that woodpeckers often respond to the call of a Barred Owl, either by vocalizing or moving closer to the source of the call (pers. observ.). This method of censusing woodpeckers has not previously been tested, although there are a few published descriptions of soliciting woodpeckers for the purpose of detection (Rushmore 1973, Wright 1991). Previous studies using fixed-radius point counts have shown that avian detections usually decrease as a function of increasing time (Scott and Ramsey 1981, Hutto et al. 1986). Thus, increases in woodpecker detections following Barred Owl hooting should represent additional detections caused by the solicitation technique.

During the 6-min period at each plot we recorded (1) time, (2) species and numbers of woodpeckers, (3) the location and movement of each woodpecker from the observer to determine the effectiveness of the owl imitation and to keep from double-counting, (4) sector (45° arcs: 0–45°, 46–90°, etc., 8 total) where each woodpecker was first detected, and (5) whether the individual woodpecker was detected in the first 3-min period, the second 3-min period, or both periods.

One entire route (20 survey plots) was censused in a single morning. Woodpeckers were censused within three hours of sunrise, which is the peak, daytime activity period for most bird species (Howell 1951, International Bird Census Committee 1970). The direction in which a route was surveyed was alternated each survey. Each site was censused twice a month throughout the year and data were pooled by year and by season: spring (March, April and May), summer (June, July and August), fall (September, October and November) and winter (December, January and February).

Vegetation data within each plot were collected during the censusing year. A total of 24 circular subplots per plot was established, three in each of the eight sectors (Fig. 1). Each

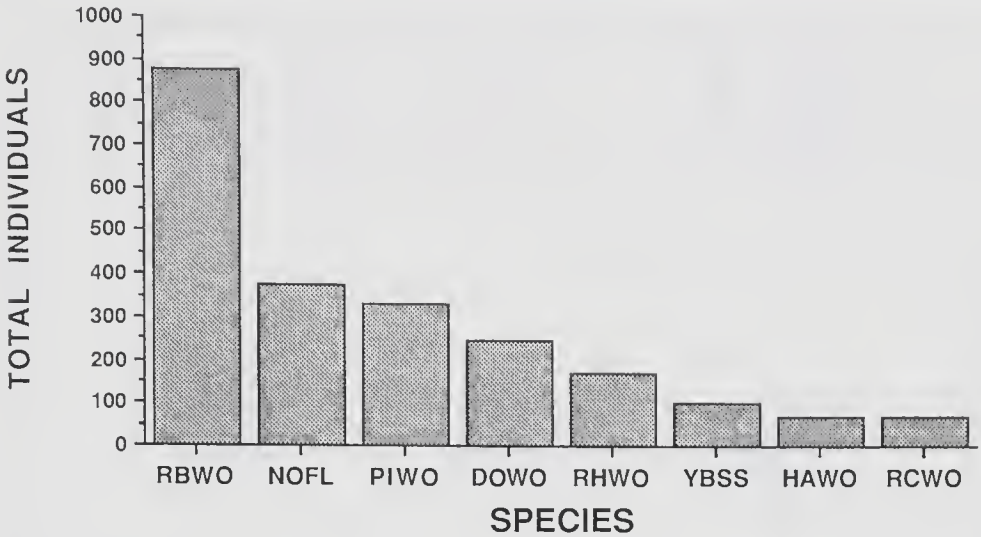

FIG. 2. The relative abundance of eight woodpecker species censused in mature forests in eastern Texas. RBWO = Red-bellied Woodpecker, NOFL = Northern Flicker, PIWO = Pileated Woodpecker, DOWO = Downy Woodpecker, RHWO = Red-headed Woodpecker, YBSS = Yellow-bellied Sapsucker, HAWO = Hairy Woodpecker, and RCWO = Red-cockaded Woodpecker. Individual woodpeckers were counted only once during each 6-min census period.

subplot had a radius of 11.2 m and an area of 0.04 ha (as described by James and Shugart [1970]; and Conner [1980, 1983]). The subplots were located along transects which bisected each sector, at a distance of 50 m, 150 m and 250 m from the center of each plot.

Forest habitat data were recorded at each of the subplots: (1) basal area of all pines and hardwoods (separately) with a one-factor metric prism and (2) number of snags and logs measured by diameter size class: sapling- (5–16 cm), pole- (17–32 cm) and sawtimber- (>32 cm) sized trees. The total number of all snags and logs of all three size classes was also recorded.

Within each forest type, we used two-tailed *t*-tests to compare vegetational characteristics between sectors where a woodpecker species was present and where the species was absent. A chi-square test for goodness of fit was used to evaluate the effectiveness of silent census-taking versus woodpecker detections following the imitation of a Barred Owl. One-way analysis of variance and Duncan's multiple range test were used to compare woodpecker abundances among habitat types.

To provide a visual comparison of the habitat used by all eight woodpecker species, we conducted a principal component analysis using all habitat variables and a varimax rotation of axes. Previous studies have successfully used principal component analysis to explore avian-habitat relationships (James 1971, Conner and Adkisson 1977, Conner et al. 1983). For comparison of woodpecker species, centroids were plotted within axes created by the first three components, and factor loadings were used to evaluate relationships of the canonical axes to original habitat variables. All analyses were calculated using PC-SAS (SAS Institute, Inc. 1988).

RESULTS

A total of 2242 woodpeckers representing eight species was detected during 144 h of observation (Fig. 2). When comparing the number of woodpeckers detected during the first 3-min (unsolicited) with the number

TABLE 1

CHI-SQUARE ANALYSES COMPARING NUMBERS OF WOODPECKERS DETECTED DURING 3-MIN OF UNSOLICITED CENSUSING AND 3-MIN OF SOLICITED CENSUSING USING THE IMITATION OF A BARRED OWL

Species[a]	Unsolicited	Solicited	% Increase	χ^2	P
YBSS	26	93	257.7	37.7	<0.01
RHWO	84	161	91.7	24.2	<0.01
NOFL	164	310	89.0	45.0	<0.01
RBWO	402	747	85.8	103.6	<0.01
DOWO	118	188	59.3	16.0	<0.01
RCWO	46	60	30.4	1.8	>0.10
HAWO	46	58	26.1	1.4	>0.10
PIWO	191	221	15.7	2.2	>0.10
Total	1077	1838	70.7	198.7	<0.01

[a] YBSS = Yellow-bellied Sapsucker, RHWO = Red-headed Woodpecker, NOFL = Northern Flicker, RBWO = Red-bellied Woodpecker, DOWO = Downy Woodpecker, RCWO = Red-cockaded Woodpecker, HAWO = Hairy Woodpecker, PIWO = Pileated Woodpecker.

detected during the second 3-min (solicited) of a census period, the imitation of a Barred Owl resulted in a 71% increase in woodpecker detections (Table 1). Some of the woodpeckers detected during the first 3-min period were also detected during the second 3-min sampling period. Chi-square analysis revealed that detections of five of the eight species increased significantly ($P < 0.01$) during the second 3-min period (Table 1). Most individuals of most species vocalized almost immediately after the first hoot was imitated by the observer. Many individuals would fly closer and perch directly over the observer's head, attempting to locate the supposed Barred Owl.

Seasonal abundance and woodpecker use of forest cover types.—Red-bellied Woodpeckers (N = 878) were the most numerous and widespread species, occurring in all three forest types each season (Fig. 3). Northern Flickers (N = 375) were second in abundance but occurred primarily during the fall and winter months, especially in bottomland hardwood forests (Fig. 3). Flickers were not permanent residents on any of the study sites. Pileated Woodpeckers (N = 334) were common throughout the year in all three forest types, while Downy Woodpeckers (N = 247) were most common in bottomland hardwood forests during summer and winter (Fig. 3). Red-headed Woodpeckers (N = 173) were present in bottomland hardwood forests only in the fall and winter, and in the longleaf pine savannah only in spring and summer (Fig. 3). Yellow-bellied Sapsuckers (N = 100) were most commonly found in bottomland hardwood forests in fall and winter, but were absent from eastern Texas in the late spring and summer

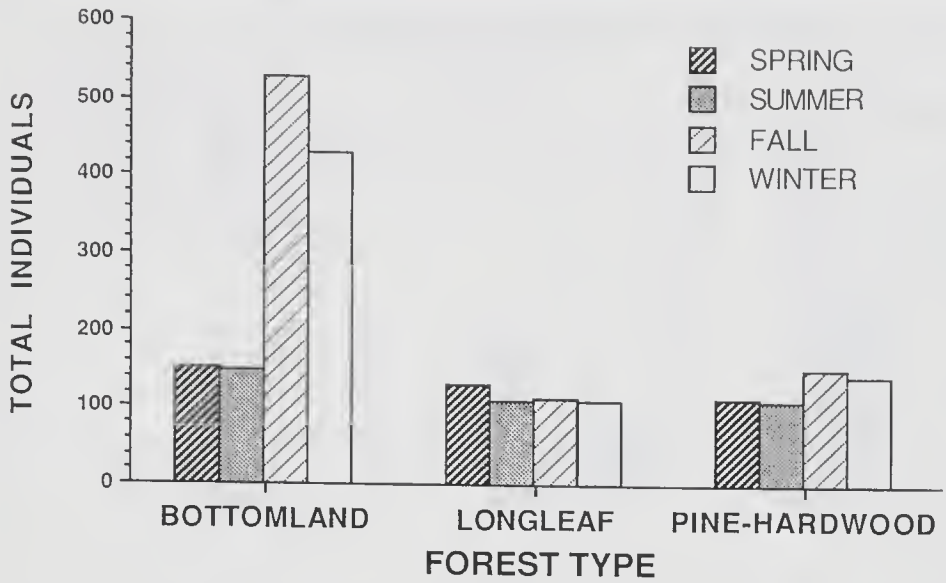

FIG. 3. Abundance of woodpecker species by season and forest type in eastern Texas. RBWO = Red-bellied Woodpecker, NOFL = Northern Flicker, PIWO = Pileated Woodpecker, DOWO = Downy Woodpecker, RHWO = Red-headed Woodpecker, YBSS = Yellow-bellied Sapsucker, HAWO = Hairy Woodpecker, and RCWO = Red-cockaded Woodpecker.

(Fig. 3). Hairy Woodpeckers (N = 68) occurred mostly in mixed pine-hardwood forests and were detected most frequently in the fall, while Red-cockaded Woodpeckers (N = 67) were found year around, but restricted to the longleaf pine savannah (Fig. 3). Hairy and Downy woodpeckers were virtually absent from the longleaf pine savannah suggesting that Red-cockaded Woodpeckers are the only regular *Picoides* occurring in these open longleaf pine sites (Fig. 3).

Numerous woodpeckers of all species, except Red-cockaded Woodpeckers, used bottomland hardwood forests during the fall and winter months suggesting the importance of this habitat type for woodpeckers during the non-breeding season (Fig. 4). Elevated woodpecker abundance during fall and winter in bottomland hardwood forests was primarily the result of migrating and wintering Northern Flickers, Red-headed Woodpeckers, and Yellow-bellied Sapsuckers in eastern Texas, as well as an increase in the number of resident Red-bellied Woodpeckers.

Significantly more Yellow-bellied Sapsuckers, Northern Flickers, Red-bellied, Downy, and Red-headed woodpeckers were detected in bottomland hardwood forests than in either of the other two forest types (Table 2). Hairy and Pileated woodpeckers were more abundant in the mixed pine-hardwood forest than the other two forest types (Table 2).

Woodpecker use of habitat in bottomland hardwood forests.—Woodpeckers, as a whole, were more abundant in bottomland hardwood forests

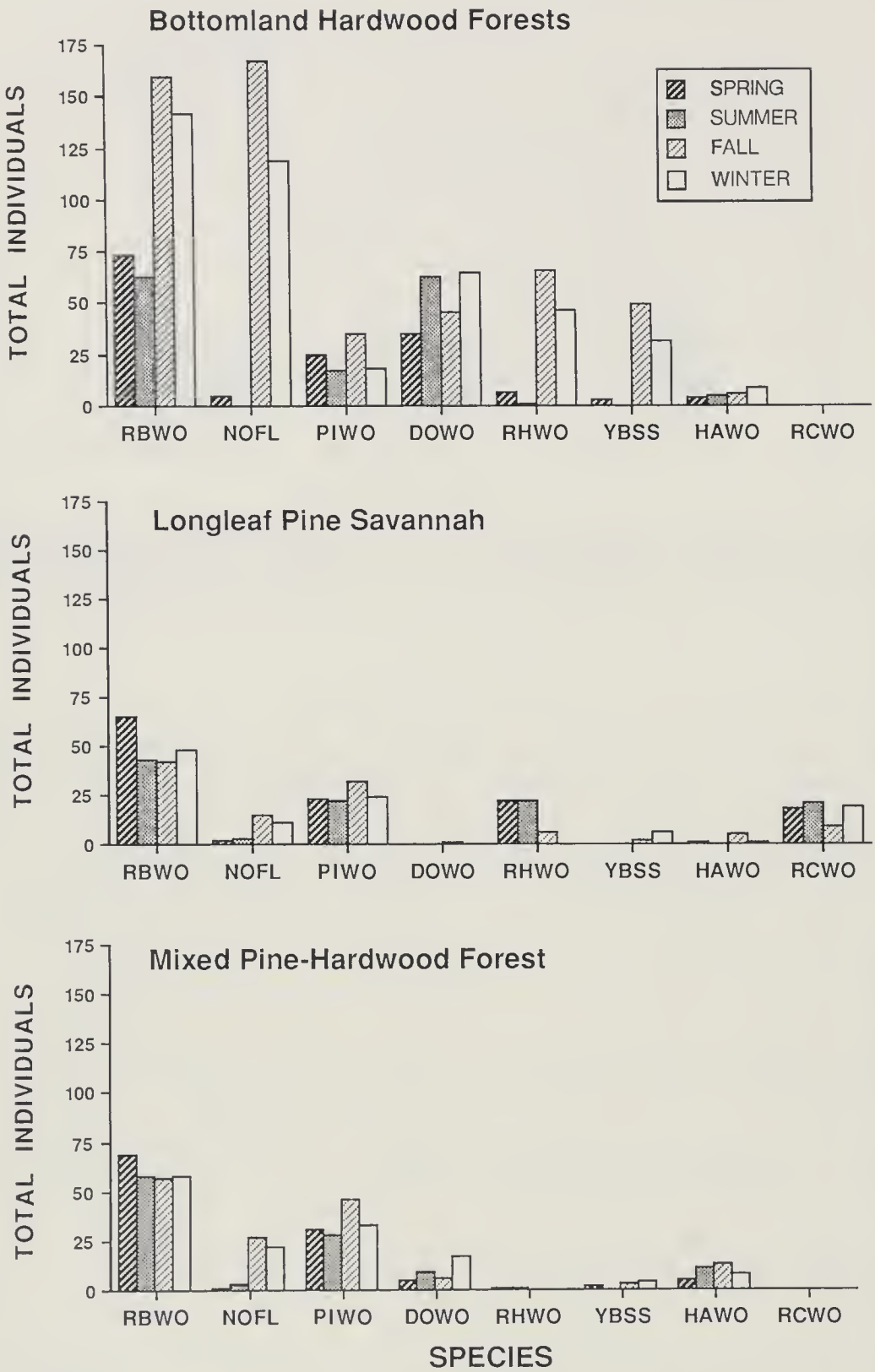

FIG. 4. Seasonal abundance of woodpeckers by forest type in eastern Texas.

TABLE 2

MEAN NUMBER OF WOODPECKERS (STANDARD DEVIATION) PER PLOT SECTOR (3.5 HA) IN THREE FOREST TYPES IN EASTERN TEXAS

Species[a]	Mixed Pine-Hardwood (N = 160)	Longleaf Pine (N = 159)	Bottomland Hardwood (N = 160)
RBWO	1.56 (2.03)a	1.26 (1.46)a	2.91 (2.05)b
NOFL	0.35 (0.71)a	0.20 (0.47)a	1.88 (1.45)b
PIWO	0.85 (1.22)a	0.64 (0.84)a,b	0.58 (0.76)b
DOWO	0.24 (0.65)a	0.01 (0.08)b	1.36 (1.27)c
RHWO	0.01 (0.11)a	0.33 (0.96)b	0.80 (1.78)c
YBSS	0.05 (0.22)a	0.06 (0.23)a	0.54 (0.98)b
HAWO	0.27 (0.70)a	0.06 (0.23)b	0.14 (0.42)b
RCWO	0.00 (0.00)a	0.46 (1.38)b	0.00 (0.00)a

[a] RBWO = Red-bellied Wodopecker, NOFL = Northern Flicker, PIWO = Pileated Woodpecker, DOWO = Downy Woodpecker, RHWO = Red-headed Woodpecker, YBSS = Yellow-bellied Sapsucker, HAWO = Hairy Woodpecker, RCWO = Red-cockaded Woodpecker. Means with common letters across a row were not significantly different from each other (One-way ANOVA and Duncan's MRT, $P < 0.05$).

than the other two forest types examined. Red-bellied Woodpeckers used areas with significantly greater numbers of sapling snags (present 0.19 ± 0.34/ha vs absent 0.08 ± 0.17/ha, $t = 2.24$, $P < 0.03$) and sawtimber logs (present 0.15 ± 0.31/ha vs absent 0.04 ± 0.10, $t = 3.02$, $P < 0.01$). During fall and winter, Northern Flickers were significantly more common in areas with sapling snags (present 0.20 ± 0.34/ha vs absent 0.07 ± 0.20/ha, $t = 2.77$, $P < 0.01$). The presence of Pileated Woodpeckers was associated with increasing numbers of pole-sized snags (present 0.14 ± 0.25/ha vs absent 0.06 ± 0.14/ha, $t = 2.53$, $P < 0.01$), sawtimber-sized logs (present 0.22 ± 0.38/ha vs absent 0.07 ± 0.19/ha, $t = 3.06$, $P < 0.01$), and total logs (present 0.35 ± 4.89/ha vs absent 0.46 ± 0.24/ha, $t = 3.53$, $P < 0.01$).

During fall and winter, Red-headed Woodpeckers were most common in areas containing high numbers of sawtimber-sized logs (present 0.35 ± 0.44/ha vs absent 0.06 ± 0.19/ha, $t = 4.10$, $P < 0.01$) and total numbers of logs (present 0.42 ± 0.45/ha vs absent 0.16 ± 0.34/ha, $t = 3.31$, $P < 0.01$). Yellow-bellied Sapsuckers were absent from areas containing a greater quantity of sawtimber-sized snags (present 0.04 ± 0.10/ha vs absent 0.08 ± 0.18/ha, $t = 2.02$, $P < 0.05$).

The presence of Hairy Woodpeckers was associated with lower hardwood basal area (present 14.50 ± 5.30 m^2/ha vs absent 17.04 ± 4.03 m^2/ha, $t = 2.48$, $P < 0.01$) and lower quantities of pole-sized snags (present 0.05 ± 0.10/ha vs absent 0.10 ± 0.21/ha, $t = 1.99$, $P < 0.05$) and sawtimber-sized snags (present 0.01 ± 0.06/ha vs absent 0.07 ± 0.17/ha, $t = 2.89$, $P < 0.01$).

Woodpecker use of habitat in longleaf pine forests.—Red-bellied Woodpeckers were absent from areas with a significantly higher basal area of pines (present 17.51 ± 2.89 m^2/ha vs absent 18.69 ± 3.86 m^2/ha, $t = 2.02$, $P < 0.05$). Northern Flickers were significantly more common in areas with sapling snags (present 0.02 ± 0.08/ha vs absent 0.00 ± 0.00/ha, $t = 2.78$, $P < 0.01$), yet were absent from areas with a significantly higher basal area of hardwoods (present 0.30 ± 0.44 m^2/ha vs absent 0.56 ± 0.91 m^2/ha, $t = 2.29$, $P < 0.02$). Pileated Woodpeckers were present in stands that had a high basal area of pines (present 18.69 ± 3.47 m^2/ha vs absent 17.32 ± 3.06 m^2/ha, $t = 2.65$, $P < 0.01$), but were absent from areas with increasing numbers of small diameter (sapling) snags (present 0.01 ± 0.03/ha vs absent 0.03 ± 0.09/ha, $t = 2.06$, $P < 0.04$).

In longleaf pine forests, Yellow-bellied Sapsuckers were absent from areas with increasing numbers of pole-sized logs (present 0.00 ± 0.00/ha vs absent 0.03 ± 0.13/ha, $t = 2.66$, $P < 0.01$), sawtimber-sized logs (present 0.00 ± 0.00/ha vs absent 0.03 ± 0.11/ha, $t = 3.38$, $P < 0.01$), and total logs (present 0.00 ± 0.00/ha vs absent 0.06 ± 0.18/ha, $t = 4.63$, $P < 0.01$), possibly suggesting the need for a sustained supply of living trees that provide an adequate supply of flowing sap. Hairy Woodpeckers were present in areas with a high pine basal area (present 20.91 ± 4.28 m^2/ha vs absent 17.76 ± 3.18 m^2/ha, $t = 2.82$, $P < 0.01$) and absent in sites without sapling snags (present 0.00 ± 0.00/ha vs absent 0.02 ± 0.07/ha, $t = 2.77$, $P < 0.01$).

Red-cockaded Woodpeckers were detected only in this forest type where their presence was significantly associated with lower basal area of hardwoods (present 0.55 ± 0.91 m^2/ha vs absent 0.09 ± 0.11 m^2/ha, $t = 2.04$, $P < 0.04$) and higher densities of pole-sized snags (present 0.09 ± 0.16/ha vs absent 0.02 ± 0.07/ha, $t = 2.26$, $P < 0.03$), total snags (present 0.15 ± 0.23/ha vs absent 0.05 ± 0.13/ha, $t = 2.14$, $P < 0.04$), and total logs (present 0.15 ± 0.25/ha vs absent 0.05 ± 0.14/ha, $t = 2.08$, $P < 0.05$).

Woodpecker use of habitat in mixed pine-hardwood forests.—Red-bellied Woodpeckers used areas in this forest type that had a significantly higher basal area of hardwoods (present 6.89 ± 3.68 m^2/ha vs absent 4.85 ± 2.56 m^2/ha, $t = 4.01$, $P < 0.01$) and were absent from areas with a significantly higher basal area of pines (present 8.49 ± 5.03 m^2/ha vs absent 10.47 ± 5.06 m^2/ha, $t = 2.30$, $P < 0.02$). Northern Flicker presence was significantly associated with higher basal area of hardwoods (present 7.22 ± 3.71 m^2/ha vs absent 5.94 ± 3.39 m^2/ha, $t = 1.99$, $P < 0.05$), numerous pole-sized logs (present 0.18 ± 0.34/ha vs absent 0.04 ± 0.14/ha, $t = 2.43$, $P < 0.02$), sawtimber-sized logs (present 0.28 ± 0.55/ha vs

TABLE 3

FACTOR LOADINGS FOR THE FIRST THREE PRINCIPAL COMPONENTS OF WOODPECKER HABITAT IN LONGLEAF PINE, MIXED PINE-HARDWOOD, AND BOTTOMLAND HARDWOOD FORESTS OF EASTERN TEXAS

Habitat variable	Factor 1	Factor 2	Factor 3
Midstory density	0.767	−0.132	−0.131
Canopy closure	0.290	−0.053	−0.112
Canopy height	0.115	0.300	−0.725
Basal area of hardwoods	0.940	−0.152	0.021
Basal area of pines	−0.939	0.108	−0.034
Basal area of sapling hardwoods	0.670	0.074	0.372
Basal area of pole hardwoods	0.630	−0.091	0.076
Basal area of sawtimber hardwoods	0.731	0.147	−0.055
Basal area of sapling pines	−0.417	0.009	0.654
Basal area of pole pines	−0.491	0.213	0.535
Basal area of sawtimber pines	−0.580	0.272	0.078
Total number of snags	0.133	0.444	0.197
Number of sapling-sized snags	0.253	0.278	0.244
Number of pole-sized snags	0.241	0.435	0.064
Number of sawtimber-sized snags	0.157	0.542	0.072
Total number of logs	0.314	0.837	−0.119
Number of sapling-sized logs	0.158	0.678	0.131
Number of pole-sized logs	0.212	0.640	−0.089
Number of sawtimber-sized logs	0.296	0.699	−0.164

absent 0.10 ± 0.26/ha, $t = 1.97$, $P < 0.05$) and total logs (present 0.57 ± 0.97/ha vs absent 0.22 ± 0.55/ha, $t = 2.13$, $P < 0.04$).

Pileated Woodpecker presence was associated with a higher basal area of hardwoods (present 7.22 ± 3.71 m^2/ha vs absent 5.94 ± 3.39 m^2/ha, $t = 1.99$, $P < 0.05$) and increasing numbers of pole-sized logs (present 0.18 ± 0.34/ha vs absent 0.04 ± 0.14/ha, $t = 2.43$, $P < 0.02$), sawtimber-sized logs (present 0.28 ± 0.55/ha vs absent 0.10 ± 0.26/ha, $t = 1.97$, $P < 0.05$), and total logs (present 0.57 ± 0.97/ha vs absent 0.22 ± 0.55/ha, $t = 2.13$, $P < 0.04$). Hairy Woodpeckers were most common in sites that had numerous sawtimber-sized snags (present 0.27 ± 0.43/ha vs absent 0.11 ± 0.26/ha, $t = 2.02$, $P < 0.05$) and sawtimber-sized logs (present 0.38 ± 0.64/ha vs absent 0.08 ± 0.21/ha, $t = 2.56$, $P < 0.02$).

Principal component analysis of woodpecker habitat.—The first six factors of the principal component analysis had significant eigenvalues (values >1.0). Although the first three components explained only 57.3% of the total variation, ordination of centroids for habitat used by the eight woodpecker species provided a meaningful graphic demonstration of differences in their habitat use (Fig. 5, Table 3). The position of the Red-

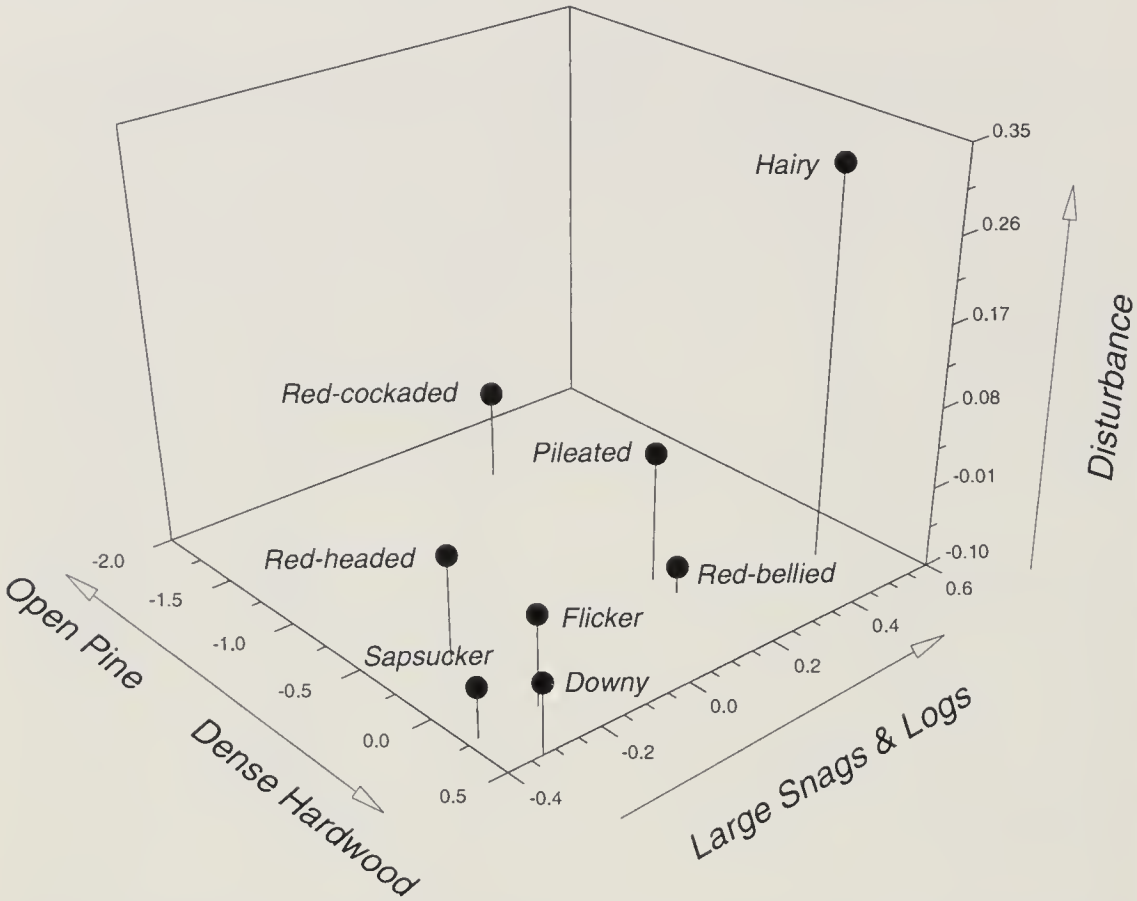

FIG. 5. Principal component analysis of habitat used by eight species of woodpeckers in eastern Texas with centroids for species plotted against the first three factors. Increasing values going left-back toward center-front (Factor 1 = "Open Pine to Dense Hardwood") represent increasing numbers, basal area, midstory density of hardwood trees, and increasing numbers of smaller-sized snags. Increasing values going center-front toward back-right (Factor 2 = "Large Snags and Logs") represent increasing numbers of large diameter logs and snags, increasing canopy height, and increasing forest maturity. Increasing values going low toward high (Factor 3 = "Disturbance") represent decreasing canopy height and increasing numbers of smaller-sized pines, characteristics associated with disturbance patches in a mature forest.

cockaded Woodpeckers' centroid is associated with pure pine stands in mature forest habitat with large diameter logs and snags present. The centroid for Hairy Woodpeckers suggests use of disturbed pine-hardwood stands where younger pines are present and large diameter snags and logs are fairly abundant. Centroids for Pileated and Red-bellied woodpeckers are associated with tall hardwood stands that have fairly high abundances of large diameter snags and logs. Centroids for Yellow-bellied Sapsuckers, Downy Woodpeckers, and Northern Flickers are associated primarily with tall hardwood stands that tend to have fewer numbers of large diameter snags and logs, but higher numbers of smaller diameter snags and logs than habitat used by the other woodpecker species.

DISCUSSION

Raphael and White (1984) observed that the diversity of cavity-nesting birds was related to snag-size diversity. Snag retention in southern forests is known to increase woodpecker diversity (Evans and Conner 1979, Dickson et al. 1983). In our study, the presence of snags and logs was associated with the habitat used by all eight species of woodpeckers. Pileated, Hairy, and Red-bellied woodpeckers were closely associated with the presence of large diameter snags and logs. Pileated Woodpeckers in Oregon (Bull and Meslow 1977) and Missouri (Renken and Wiggers 1989, 1993) used forests with numerous snags and logs. Throughout their range, Pileated Woodpeckers use snags for nesting and roosting, and snags and logs as foraging sites (Bull 1975, Conner et al. 1975, McClelland 1979, Mannan et al. 1980). In our study Red-headed Woodpeckers and Northern Flickers were associated with increasing numbers of small diameter snags. It is unclear why they were not more closely associated with large diameter snags because both species are known to use large diameter snags regularly for nesting (Conner et al. 1975, Conner 1976, Jackson 1976, Ingold 1989).

Forest age also influences habitat use by woodpeckers. Hairy, Red-bellied, Pileated, and Red-cockaded woodpeckers were associated with older-growth forest habitat. The Red-cockaded Woodpecker's requirement for old-growth forests is well known (Jackson and Jackson 1986, Rudolph and Conner 1991, Conner et al. 1994b). In Oregon, Pileated Woodpeckers selected mature forest habitat age-classes greater than 70 years of age, and selected against forest habitat age-classes less than 40 years of age (Mannan 1984, Mellen 1987, Mellen et al. 1992). Other studies suggest that mature and old-growth forests are as important to Pileated Woodpeckers as the availability of dead wood (Kilham 1976, Conner 1980, Mannan 1984, Bull and Holthausen 1993). These features, mature forest and dead wood, are usually found together in forests that have been affected minimally by humans (Thomas et al. 1988).

The presence of hardwood trees was associated with the occurrence of all woodpecker species except the Red-cockaded Woodpecker. Bottomland hardwood forests were heavily used by Northern Flickers, Yellow-bellied Sapsuckers, and Red-bellied and Red-headed woodpeckers during fall and winter. Abundant acorn crops have been associated with woodpecker use of bottomland hardwood forests (Kilham 1958). Red-headed Woodpeckers favor open park-like woodlands for nesting (Bock et al. 1971, Conner 1976). This species tends to be a short-range migrant and when breeding habitat does not contain abundant mast for winter forage, Red-headed Woodpeckers often concentrate in bottomland hardwood for-

ests (Kilham 1958, Bock et al. 1971, Moskovits 1978, Conner et al. 1994a). Downy Woodpeckers were also most abundant in bottomland hardwood forests, and were virtually absent from longleaf pine savannah. Consistent with previous studies (Bent 1939, Reller 1972, Conner 1980, Short 1982), Red-bellied Woodpeckers were more commonly detected in hardwood stands than in pine stands. Consistent with the observations of our study, Red-cockaded Woodpeckers are typically found in the open, fire-disclimax, mature-pine ecosystems of the southeastern United States where hardwood occurrence is reduced by fire (Hooper et al. 1980, Conner and O'Halloran 1987).

Disturbances in mature forest habitat benefited only one of the woodpecker species we studied. Hairy Woodpeckers occurred most frequently in mature, mixed pine-hardwood forests, especially in the residual trees of small disturbances associated with pine bark beetle infestations and timber thinning activities. Hairy Woodpeckers are seldom abundant, but occur in a wide range of habitats (Bent 1939, Short 1982). In New York (Kisiel 1972) and Virginia (Conner 1980), Hairy Woodpeckers used forests with more hardwoods than conifers, but in Colorado they used forests with more conifers than hardwoods (Stallcup 1968).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Woodpecker abundance was primarily influenced by the presence and numbers of live hardwood trees, snags, and logs. Management for woodpeckers in mixed pine-hardwood forests should encourage provision and maintenance of large diameter snags and logs as well as a balance of hardwoods and pines. Management for woodpeckers in the longleaf pine savannah should encourage the maintenance of a greater basal area of mature pines and numerous large diameter snags and logs. The continuous use of prescribed fires should be employed to keep pioneering hardwoods to a minimum, thus maintaining the savannah condition. Management for woodpeckers in bottomland hardwood forests should include provision of a mature overstory where trees are left to die of natural causes supplying woodpeckers with a sufficient number of both small and large snags and logs.

Imitating the call of a Barred Owl increased detections of woodpeckers relative to the numbers detected when the observer was silent, but did not work equally well on all species. Because of the large home range of many woodpecker species and their often difficult detection, owl "hooting" by census takers should be considered during future studies on woodpeckers as a possible means to provide a more complete sample of woodpecker populations. It is likely that different species of owls should be used in different geographic locations to get the same mobbing effect.

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NON-BREEDING TERRITORIALITY OF SEMIPALMATED SANDPIPERS

KIMBERLY J. TRIPP[1,2] AND JAIME A. COLLAZO[1]

ABSTRACT.—We studied non-breeding territorial behavior of Semipalmated Sandpipers (*Calidris pusilla*), and documented the proportion of individuals of Least (*C. minutilla*) and Western (*C. mauri*) sandpipers exhibiting territoriality during fall of 1994 and 1995 at the Cabo Rojo salt flats, Puerto Rico. Territoriality was exhibited by 8–19% of the population, with Least Sandpipers exhibiting the highest proportion of all three species. The prevalence and size of territories of Semipalmated Sandpipers was influenced by the availability of high prey density sites, bird density, and aggression levels. Individuals defended territories in areas of highest prey densities (0.16 ± 0.009 /cm^3). Non-territorial birds, however, foraged in areas of significantly higher prey densities (0.02 ± 0.001 /cm^3) than overall lagunal levels (i.e., randomly sampled plots) (0.006 ± 0.009 /cm^3). Territorial Semipalmated Sandpipers spent less time foraging than non-territorial birds (1994: 90 vs 36%; 1995: 85 vs 55%). They also spent less time in maintenance behavior (i.e., preening). Costs of territoriality may be offset by foraging in areas of high prey densities or through increased foraging efficiency. Prey density did not exert a direct influence on territory size ($P = 0.67$). Rather, it influenced territory size through effects on aggression. Territory size was inversely related to the mean time spent on aggression ($P < 0.001$). Territory size was also inversely related to bird density ($P < 0.001$), a factor that might contribute to higher incidence of aggressive bouts. These findings support the contention that a facultative strategy with respect to non-breeding territorial behavior seems to offer migratory species the flexibility to cope with spatio-temporal fluctuations of prey resources and shorebird density. *Received 12 Nov. 1996, accepted 22 April 1997.*

Migratory shorebirds spend over half of their annual cycle at staging areas and wintering grounds (Gochfeld et al. 1984). During this period, they must satisfy high energetic demands (e.g., molt, migratory flights) in the face of variable environmental conditions (e.g., food resources, weather, predation) (Pienskowski and Evans 1984, Senner and Howe 1984, Myers et al. 1987). These conditions may increase the risk of mortality, justifying emphasis on the migratory and wintering periods in discussions of shorebird population regulation (Myers et al. 1985, Myers et al. 1987). Shorebirds have developed several strategies to cope with such energetic demands. At a hemispheric level, they rely on a few vital links that serve as resting and foraging areas (Myers et al. 1987). At a local level, shorebirds distribute themselves where prey items are most abundant (Hicklin and Smith 1984, Grear 1992). Within these patches, some shorebird species select the most energetically profitable prey items (e.g.,

[1] North Carolina Cooperative Fish and Wildlife Research Unit, Biological Resources Division, U. S. Geological Survey, North Carolina State Univ. Raleigh, North Carolina 27695.
[2] Current address: U.S. Fish and Wildlife Service, Raleigh Field Office, Raleigh, North Carolina 27606.

by size or prey type) (Goss-Custard 1970, 1977; Goss-Custard et. al. 1977). Furthermore, if prey are defendable, some individuals will assert exclusive claim over food resources through territorial behavior (Brown 1964, Recher 1966, Myers et al. 1979a).

Territoriality in non-breeding shorebirds has been documented at migratory stopovers and wintering areas in northern latitudes (Hamilton 1959, Myers 1979a, Connors et al. 1981) as well as on their tropical wintering grounds (Duffy et al. 1981, Myers and McCaffery 1984). Yet, despite its widespread occurrence, the benefits of engaging in non-breeding territorial behavior are not well understood (Myers et al. 1979a, Myers 1984). Costs associated with the establishment and maintenance of territories are high, sometimes at the expense of essential activities such as foraging and maintenance. It is believed that territorial individuals attain a higher net energetic gain than non-territorial shorebirds (Brown 1964, Verner 1977); however, there has been no conclusive evidence to support this contention (Myers et al. 1979a, Myers 1984). The trade-offs between energetic gains and costs of territorial defense can be reflected in the variability of territory size (Myers et al. 1979b). For instance, Myers (op. cit.) showed that Sanderlings (*Calidris alba*) will defend an area as large as competition permited. This finding suggested that prey density was not the sole determinant of territory size as previously hypothesized (Stimson 1973, Brown 1975, Gass et al. 1976). Myers et al. (1979b) demonstrated that territory size varied inversely with prey density. The inverse relationship resulted from the determining influence of an intervening factor, intruder density. Unfortunately, lack of information on other species precluded Myers et al. (1979b) from making generalizations about their territory size model.

Identifying components of non-breeding territoriality shared among species is necessary to gain insights about its possible adaptive significance. Meeting this need has been hampered by the dearth of information on non-breeding territoriality. In this study, we test whether Myers' et al. (1979b) model of Sanderling non-breeding territoriality is applicable to Semipalmated Sandpipers (*Calidris pusilla*) at the Cabo Rojo salt flats, Puerto Rico. Specifically, we tested whether prey density had a regulatory effect on territory size or whether territory size was mediated by intruder density. Other components of non-breeding territoriality were examined in order to develop a broader base for generalizations and aid in the interpretation of costs and benefits of territoriality. To this end, we tested or documented (1) whether prey densities on defended territories differed significantly from those on adjacent areas where territoriality was not exhibited, (2) the allocation of time to selected activities by territorial and non-territorial individuals, and (3) the prevalence of territorial individuals

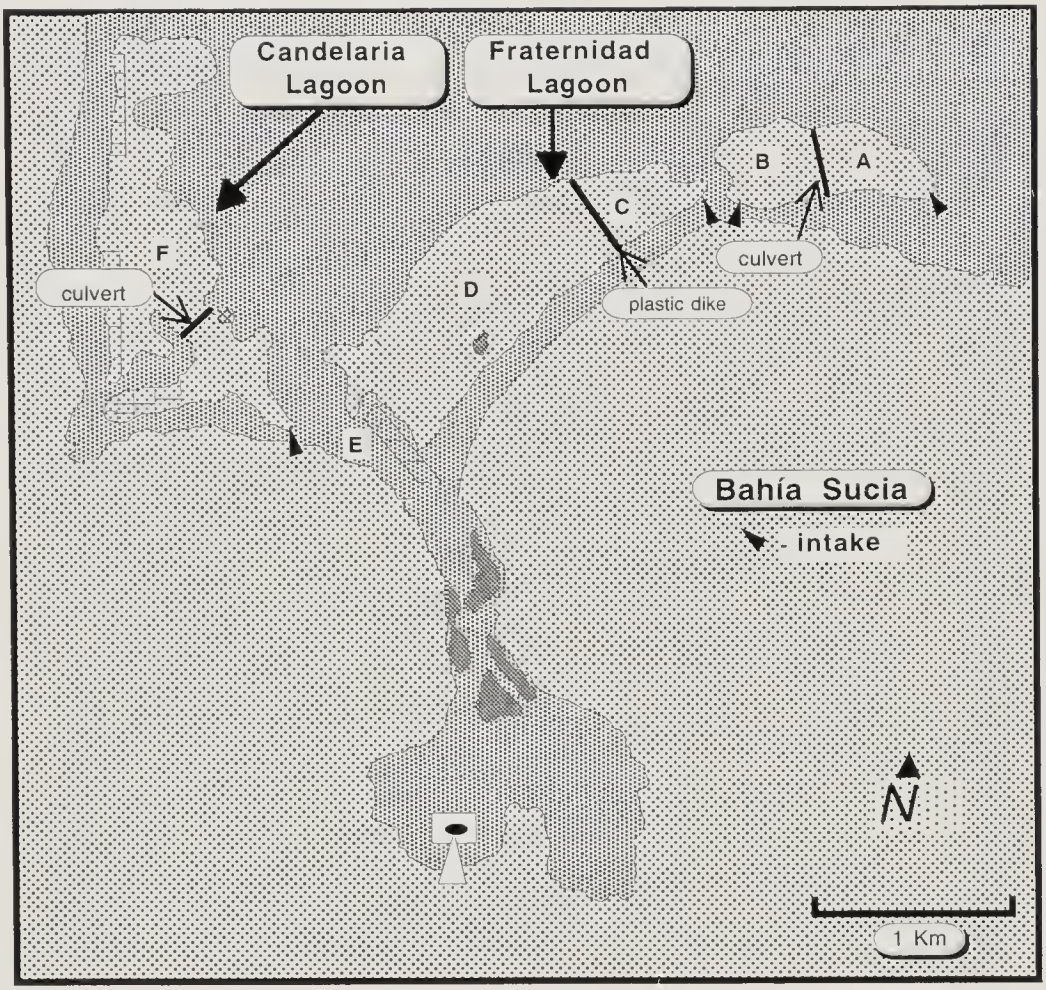

FIG. 1. Map of the Cabo Rojo salt flats, Puerto Rico showing sampling areas (A–F) in the Fraternidad and Candelaria lagoons. Shorebird observations were made along the northwest shore of area A (1994) and the north shore of area D (1995).

in the population, including observations on Least (*Calidris minutilla*) and Western (*Calidris mauri*) sandpipers.

STUDY AREA AND METHODS

This study was conducted at the Cabo Rojo salt flats in southwest Puerto Rico (67°12′ N, 18°57′W) (Fig. 1). Two large shallow lagoons, Fraternidad and Candelaria, covering approximately 445 ha are the most striking features of the area. Strips of littoral vegetation, dirt, and paved roads delineate most of the salt flats and roads provide access to nearly every location. Mean (±SE) water depth (cm) per area was 5.3 ± 0.2 (A), 5.7 ± 0.2 (B), 16.2 ± 0.5 (C), 15.3 ± 0.4 (D), and 16.2 ± 0.4 (F) (Fig. 1). Size (ha) estimates of sampling areas were A (17.4), B (19.0), C (72.3), D (10) and F (26.2). Data presented herein were collected in areas A and D of Fraternidad Lagoon. These areas encompassed the range of salinity levels in the system, hosted two primary prey species, and were accessible (i.e., depth range) to foraging Calidrids (Grear 1992, Tripp 1996). Prey species were water boatmen (*Trichocorixa reticulata*), found exclusively in area A, and brine shrimp (*Artemia* spp.), found only in area D.

Observational data were collected on the north shore of area D from September 8 through 25, 1995. The shoreline was divided into seven 100 m strip sections identified either by stake markers or landmarks. Each day, a section of shoreline was randomly chosen for observations. We stood 50 m from the left end of the selected section and used focal and scan sampling to collect behavioral information (Altmann 1974). Scans were used to determine the proportion of birds in the flocks engaged in territorial behavior. Focals were used to determine the percentage of time selected individuals were engaged in distinct behaviors. We initiated observation periods with a scan of the selected sampling area, recording species composition, numbers of small calidrids, and the number of territorial birds with the aid of binoculars. Shorebirds were considered territorial if they exhibited behaviors such as vigilance in response to potential intruders or aggressive displays associated with boundary disputes. Upon completing the scan, we selected the first territorial bird (i.e., focal) looking from left to right within the area of interest and recorded the total number of shorebirds within a 10 m radius of the focal individual. We then recorded the focal bird's behavior for a total of three minutes (Ashmole 1970). Behaviors were classified according to the following categories (adapted from Hamilton 1959): vigilance (alert posture with neck stretched upwards and legs straightened), aggression (threat posture with head down and rump raised, or an attack where a bird either rushes across the ground or flies at an opponent, displacement (the act of a bird chased away from a location), foraging (searching, handling and ingestion of prey), and preening (cleaning its feathers).

Territories were linearly arranged along the shoreline with widths not exceeding 1 m. Territory dimensions were estimated on the basis of the locations of other birds which elicited an aggressive stance or attack from the territorial bird (Myers et al. 1979b). After completing the focal sample, we selected the first non-territorial bird seen ≥2 m into the lagoon from the territorial bird. Non-territorial birds were usually found away from the shoreline in deeper waters. We then collected data in the same manner and also added the behavioral category of displacement. After completing observations on a pair of territorial and non-territorial birds, we shifted our observation focus 10 m down the shoreline and selected the next territorial bird. If any focal birds left the area before the 3-min period ended, we omitted the observation and selected another individual.

The location of each focal bird was carefully noted using stakes placed in the lagoon or other landmarks used as reference points. After every three paired observations of territorial and non-territorial birds, we sampled prey at each location. Sandpipers were observed foraging only in the water column (Tripp 1996) to which we restricted prey sampling. Prey were sampled using a plastic cylinder 15 cm in diameter. Upon approaching the area of interest (i.e., first location noted for each focal), we extended our arms (0.5–0.9 m from our torso), dropped the cylinder and pushed it into the substrate to minimize prey loss. We then measured the depth of water, filtered the trapped water through a 1 mm mesh sieve (Bengston and Svennson 1968), and counted and identified the types of organisms within the sampled volume of water. After this process was completed, we initiated another set of three paired observations of territorial and non-territorial birds, starting from the point along the 100 m transect where the last set of observations was made. For each 100 m strip of shoreline, a total of nine sets of paired observations were made, each with respective data on prey availability. Estimates of lagunal prey levels were obtained from four sampling plots established throughout area D (Tripp 1996). Plot dimensions were 50 m × 30 m. Each plot was divided into six divisions along the shoreline and three subdivisions perpendicular to the shoreline. Every plot was sampled once a week. Each week, two divisions were selected randomly. From each selected division, two samples from each of two randomly chosen subdivisions were collected. Subdivisions were sampled without replacement. Prey was processed as described above for territorial and non-territorial locations. In all cases, it is

possible that prey estimates were biased low (e.g., prey moving away from approaching sampler); however, sampling was standardized, and thus comparisons were made on the basis of precise estimates.

From September to November 1994 behavioral data were also collected on the northwest shoreline of area A. This area was divided into five 50 × 10 m sections. Each day a section was randomly chosen. Scan and focal behavioral data were collected as in 1995. Differences between years were in the number of scans performed and how the focal bird was selected. In 1994, scans were done every hour. Focal birds were selected by focusing binoculars in the center of the observation area and selecting the bird to the right of the center of the field of view. Subsequent focal birds were selected by choosing an individual about 10 m to the right or left of the previous focal bird to minimize observing the same bird.

A paired *t*-test was used to test whether there were differences in prey density (individuals/cm^3) or bird density between territorial and non-territorial sites. Unless otherwise specified, bird density is defined as number of birds within a 10 m radius of focal birds. The 10 m was estimated with the aid of stakes and landmarks in the observation area. Territory sizes (m) (i.e., linear dimension) between areas A and D, and percent of time spent by territorial and non-territorial individuals on selected behavioral categories were compared using Wilcoxon tests (JMP 1994). Because shorebird density can influence territory size (Myers et al. 1979b), comparisons between areas A and D were made only when the number of shorebirds per area were comparable (i.e., adjusting by density). Averages were reported as mean ± standard error.

Path analysis was performed on 1995 data (sensu Myers et al. 1979b). To conduct the analysis, standardized values of the inverse of territory length (1/TL), the response variable, were regressed on the percentage of aggressive activity (AGG) and prey density (PD), the independent variables, using multiple regression. The inverse of "TL" was used because a hyperbolic relationship between prey density and territory size was expected (Gass et al. 1976, Myers et al. 1979b). The relationship between PD and AGG was determined using a simple regression analysis. Standardized regression coefficients indicate the strength of the relationships among the variables of interest (Mitchell 1993). Unlike Myers et al. (1979b), we used the mean total time spent in aggression as an index of territory defense (i.e., AGG) because shorebirds were not individually marked. Territorial birds attack or display towards trespassers in various ways, from short-lived threatening stances to prolonged physical attacks. Therefore, we believe that mean total time spent in aggression was a good indicator of the extent to which a bird defended a territory. Simple regression analysis was used to examine if the relationship derived from 1995 data between AGG and 1/TL was also observed in 1994. All tests were considered significant at an alpha of ≤0.05.

RESULTS

Semipalmated Sandpipers monitored in areas A and D accounted for 61% (1994) and 80% (1995) of the birds. Western Sandpipers and Least Sandpipers were second in abundance in 1994 and 1995, respectively. Within the flocks observed during the study, 8% to 19% of the birds exhibited territorial behavior (Table 1). On the average, Least Sandpipers comprised the highest proportion of territorial birds. Proportion of territorial birds varied markedly for Semipalmated Sandpipers between 1994 and 1995 but not for Western or Least Sandpipers.

Territories of Semipalmated Sandpipers consisted of rectangular strips along the shoreline, ranging from 3.30 ± 0.19 m in 1994 (N = 53) to

TABLE 1

MEAN (±SE) NUMBER PER SCAN SAMPLE OF LEAST (LESA), SEMIPALMATED (SESA) AND WESTERN (WESA) SANDPIPERS AT THE CABO ROJO SALT FLATS, PUERTO RICO IN 1994 AND 1995

Year	Mean number per scan	Mean percent of total numbers by species			Mean percent territorial of total numbers[a]	Mean percent territorial birds within a species[b]		
		LESA	SESA	WESA		LESA	SESA	WESA
1994	126.6 ± 7.0	19.8 ± 2.9	60.8 ± 4.6	19.5 ± 4.8	8.5 ± 7.9	15.2 ± 4.9	5.3 ± 2.7	2.3 ± 0.6
1995	62.9 ± 0.9	16.6 ± 2.6	79.8 ± 3.7	5.7 ± 1.9	18.5 ± 0.9	12.4 ± 6.4	14.0 ± 3.8	4.4 ± 1.2

[a] Territoriality is expressed as the mean (± SE) percent of the total number of birds exhibiting territoriality.
[b] Territorial behavior broken down by species and expressed as the mean (± SE) percent of birds within a species exhibiting territoriality.

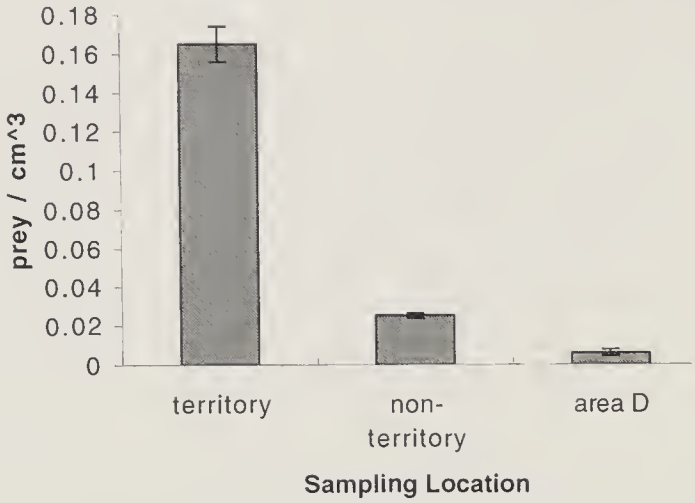

FIG. 2. Mean (±SE) brine shrimp/volume sampled in territory and non-territory sites of Semipalmated Sandpipers and randomly sampled plots in area D at the Cabo Rojo salt flats, Puerto Rico.

4.80 ± 0.31 in 1995 (N = 55). Territory length was linearly but negatively related to bird density (1994-area A: F = 45.03, d.f. = 1, 51; $P < 0.001$, $R^2 = 42\%$; 1995-area D: $F = 14.37$, df = 1, 53; $P < 0.001$, $R^2 = 22\%$). Adjusting for bird density, territory length was not significantly different between areas ($\bar{x}$ A = 5.00 ± 0.85; $\bar{x}$ D = 4.70 ± 0.28; $\chi^2 = 0.66$, P = 0.42). Prey density levels in territories ($\bar{x}$ = 0.16 ± 0.009/cm^3) were significantly higher than in areas where no territoriality was exhibited ($\bar{x}$ = 0.02 ± 0.001/cm^3; $t = -15.10$, df = 64, $P < 0.001$). Areas used by non-territorial birds had significantly higher prey densities than randomly sampled plots in area D ($\bar{x}$ = 0.006 ± 0.009/cm^3; $\chi^2 = 40.88$, P < 0.001) (Fig. 2). Bird density within a 10 m radius of focal birds was significantly greater around non-territorial birds ($\bar{x}$ = 17.36 ± 1.12) than territory holders ($\bar{x}$ = 12.17 ± 0.72; $t = 3.65$, df = 56, $P = 0.0006$).

Time spent on aggression by territorial Semipalmated Sandpipers ranged from 26% in 1995 to 47% in 1994 (Table 2). Time spent in aggression and density of birds were significantly and positively related (1994-area A: $F = 18.96$, df = 1, 51, $P < 0.001$, $R^2 = 27\%$; 1995-area D: $F = 49.55$, df = 1, 53, $P < 0.001$, $R^2 = 48\%$). As time spent in aggression increased, territory length decreased (1994-area A: $F = 46.33$, df = 1, 51; $P = 0.001$, $R^2 = 48\%$; 1995-area D: $F = 82.63$, df = 1, 53; $P < 0.001$, $R^2 = 61\%$). There was a significant inverse relationship between the number of territorial birds and the total number of birds counted within a 50 m × 10 m area ($F = 6.84$, df = 1, 13; $P = 0.02$, $R^2 = 35\%$) (Fig. 3). Territorial birds spent significantly less time foraging (1994: $\chi^2 = 103.14$, $P < 0.001$; 1995: $\chi^2 = 55.23$, P < 0.001) and preening (1994: $\chi^2 = 9.19$, P = 0.002; 1995: $\chi^2 = 38.39$, P < 0.001) than did non-

TABLE 2

MEAN (± SE) PERCENT OF TIME SPENT ON SELECTED BEHAVIORAL ACTIVITIES BY TERRITORIAL AND NON-TERRITORIAL SEMIPALMATED SANDPIPERS IN 1994 AND 1995 AT THE CABO ROJO SALT FLATS, PUERTO RICO

	Territorial (N = 188)		Non-territorial (N = 115)	
Behavior[a]	1994	1995	1994	1995
Aggression	47.4 ± 2.5	25.5 ± 1.5	0	0
Preening	0	0	6.9 ± 1.8	11.3 ± 2.1
Vigilance	17.4 ± 2.1	19.9 ± 2.2	0.5 ± 0.2	2.5 ± 0.9
Foraging	35.2 ± 2.7	54.5 ± 2.2	89.8 ± 1.95	85.1 ± 2.2
Displacement	0	0	2.81 ± 0.8	1.0 ± 0.5

[a] Percentages estimated on the basis of 3-min focal samples. Behavioral activities adapted from Hamilton (1959).

territorial birds in both years (Table 2). Conversely, they spent more time in vigilance than non-territorial birds (1994: $\chi^2 = 97.62$, $P < 0.001$; 1995: $\chi^2 = 41.93$, $P < 0.001$) and were the only individuals to exhibit aggression.

Aggression (AGG) had a strong effect on territory size (1/TL) (stand. partial coef. = 0.82, df = 1, 52; $P < 0.001$, R^2 for multiple regression = 71%) (Fig. 4). Similarly, prey density had a strong effect on aggression (stand. coef. = 0.60, $P < 0.001$, $R^2 = 39\%$). In contrast, prey density had little effect on territory size (stand. partial coef. = 0.04, df = 1, 53; $P = 0.67$). The relationship between 1/TL and AGG in 1994 was consistent with the relationship found in 1995, that is, they were linearly and

FIG. 3. Number (and percentage) of territorial Semipalmated Sandpipers recorded at different bird densities at the Cabo Rojo salt flats, Puerto Rico, in 1994 and 1995.

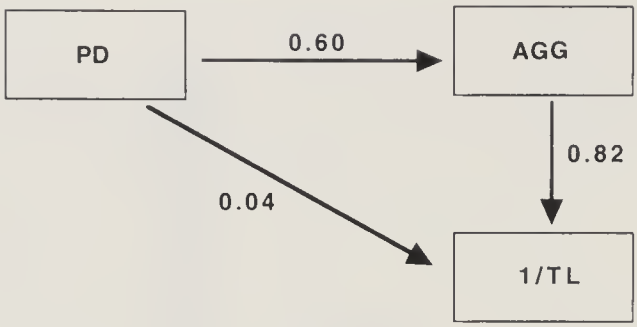

FIG. 4. Path diagram showing the relationship between prey density (PD), mean total time spent on aggression (AGG), and territory length (TL) exhibited by Semipalmated Sandpipers at the Cabo Rojo salt flats, Puerto Rico. Path coefficients are standardized partial regression coefficients predicting 1/TL from PD and AGG. Path coefficient predicting AGG from PD is a standardized regression coefficient.

positively related (stand. partial coef. = 0.69, df = 1, 51; $P < 0.001$, $R^2 = 48\%$).

DISCUSSION

Areas held by territorial Semipalmated Sandpipers had significantly higher prey densities than areas held by non-territorial birds, and foraging sites used by non-territorial birds had higher prey densities than randomly sampled lagunal plots. These findings were consistent with the hypothesis that shorebirds should distribute themselves according to the prey density distribution (see Hicklin and Smith 1984). Findings also indicate two levels of habitat selection. Food was most abundant where flocks of birds occurred (i.e., mix of territorial and non-territorial individuals), as compared to randomly sampled plots in area D. A similar pattern was reported by Grear (1992). Moreover, territorial birds selected prey patches at a scale which hosted the highest overall prey density. This suggests that territorial birds defend patches of abundant food resources which might confer unique energetic benefits to the territory holder (Brown 1964, Myers et al. 1979a).

The relationship among territory length, aggression, and prey density suggests that inferences made by Myers et al. (1979b) for Sanderlings can be extended to include Semipalmated Sandpipers. Accordingly, our findings support the hypothesis that this species will defend territories as large as competition permits. Prey density did not exert a strong effect on territory size. The weak relationship had its basis in the fact that levels of aggression increased in areas of highest prey densities, likely due to the fact that bird density also increased with prey density. As bird density increased, the number of territorial birds decreased significantly. This relationship was true both for brine shrimp (area D) and water boatmen

(area A). Similar findings have been documented for Great Tits (*Parus major*), where year to year variation in territory size is related to the number of birds seeking territories rather than variations in prey density (Krebs 1971).

Myers et al. (1979a) identified three concurrent levels of prey density and documented territoriality only at intermediate levels. They hypothesized that at higher prey densities (e.g., superabundant resources) territories could not be defended due to the high frequency of intrusions caused by the higher concentration of shorebirds (see also Brown 1964). Consistent with Myers et al. (1979a) findings, we found expressions of territoriality lessened with increasing bird density. Decreasing territoriality, however, was not associated with a third level of prey density (e.g., superabundant). We only identified two levels of prey density, with territoriality always associated with areas of highest densities. As birds discovered these sites, their densities increased to levels where territorial defense was no longer possible. Further evidence that a superabundant level of prey abundance was not present at the salt flats was that the highest bird densities were associated with non-territorial birds. These birds foraged in areas of lower prey densities than territorial birds, albeit not as low as the overall background levels (i.e., random samples) in the salt flats. Differences between Myers (op. cit.) findings and our study may be accounted for by differences in prey species and system productivity.

Our findings raise questions about the adaptive significance of non-breeding territoriality, as did those of Duffy et al. (1981, 1984) and Myers (1984). Territory holders have nearly exclusive access to higher than average prey concentrations. To gain this privilege, however, they spent large amounts of time on aggression and vigilance and reduced preening time. Possibly, prey intake is increased to compensate for lost time in aggression and vigilance (Mallory and Schneider 1979, Goss-Custard 1984). Studies of marked populations (i.e., Sanderlings, Myers et al. 1979b), however, also suggest that not all individuals are territorial, and those that are exhibit a great deal of variability in their expression of it (e.g., hours to months). This suggests that territoriality is not the only strategy that migrant shorebirds use to meet their energetic demands and that energetic gains derived from territoriality could be accrued by a mix of short and long-term bouts. When territoriality is not possible, individuals could draw upon the extra time not invested in territorial defense to ensure adequate energy-intake and maintenance. The persistence of this alternative strategy in the population probably has its basis in the ability of non-territorial individuals to maximize their energy intake by foraging in areas that, although not as good as terri-

tories, still have relatively higher prey concentrations than randomly sampled plots as shown in this study.

Why is non-breeding territoriality not more prevalent in the population? In the salt flats, the proportion of territorial individuals of three species of small calidrid sandpipers ranged from 8–19%. One possibility is that while being territorial might yield greater benefits, establishing territories can occur only at certain levels of prey density. Moreover, if the area where such conditions prevail is spatially limited, the number of territories would be constrained as well. Our observations were consistent with these possibilities. Territoriality was observed only in a few shoreline locations with relatively high concentrations of prey. These patterns could be explained, in part, by the resultant effect of prevailing winds (i.e., east, south-east) and their variable speeds which accumulated prey along the shoreline region (Tripp and Collazo 1995). Our observations suggest that shifts from territoriality to vagility (i.e., longevity of territories) were likely adjustments to spatio-temporal fluctuations in resource availability (Connors et al. 1981, Duffy et al. 1981, Myers 1984).

Least Sandpipers consistently exhibited more territoriality than did Semipalmated or Western sandpipers. This pattern is interesting because Least Sandpipers are restricted to shallow waters by virtue of their size (2 cm tarsometatarsus). As such, they often forage amidst dense, mixed-species flocks. Aside from species-specific differences in behavior, higher expressions of territoriality were probably facilitated by their relatively low numbers and the fact that Semipalmated and Western sandpipers can scatter themselves over a wider range of foraging depths, hence, minimize the potential number of intrusions into territories. Least Sandpipers might also be responding to patterns of prey composition and dispersion along the wet and submerged transition zone of shorelines not found in deeper waters exploited by Semipalmated and Western Sandpipers.

Hypothesized benefits and costs of non-breeding territoriality need to be judged on the basis of demographic effects (e.g., survivorship rates) and population regulatory functions (Myers 1984). Information on the former is lacking and evidence for the latter is equivocal (Duffy et al. 1981, 1984; Myers 1984, Myers and McCaffery 1984). There is agreement, however, that migrant shorebirds face high energetic demands (Myers 1984, Myers et al. 1987). The findings of our study support Connors' et al. (1981) contention that a facultative strategy with respect to non-breeding territorial behavior seems to offer migrant shorebirds the flexibility to cope with spatio-temporal fluctuations in resource availability and bird density.

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WITHIN-SEASON DISPERSAL, NEST-SITE MODIFICATION, AND PREDATION IN RENESTING HOODED WARBLERS

JOAN S. HOWLETT[1] AND BRIDGET J. M. STUTCHBURY[2]

ABSTRACT.—To test the hypothesis that within-season dispersal and nest-site modification (e.g., changes in nest concealment) occur in Hooded Warblers (*Wilsonia citrina*) as a result of predation of the previous nest, we examined differences in nest height, vegetation density surrounding the nest, nest visibility, and distances between first and second nests. The average distance between successful nest sites and renesting sites was significantly greater than the average distance between unsuccessful nest sites and renesting sites. The concealment variables of renesting sites were not significantly different from either successful or unsuccessful first nest sites. The probability of success of a Hooded Warbler's renest after predation was the same as the probability of success of all first nests (approximately 50%). Our data suggest that predation does not play a role in the selection of renesting sites in Hooded Warblers. We propose that the greater dispersal of successful females was due to their avoidance of fledglings that remained near the nest with the male. *Received 30 Oct. 1996, accepted 10 May 1997.*

Birds that raise multiple broods in a season, or suffer predation and renest, can locate a new nest close to the original site or they can disperse. The factors selecting for within-season dispersal are not well known, but it has long been assumed that nest predation may have an influence (Darley et al. 1971, Greenwood and Harvey 1982). In this case, dispersal is viewed as a predation-avoidance tactic.

Several open nesting species move long distances and/or abandon territories and mates after nest failure (e.g., White-crowned Sparrow [*Zonotrichia leucophrys*, Blanchard 1941]; Gray Catbird [*Dumatella carolinensis*, Darley et al. 1971]; Prairie Warbler [*Dendroica discolor*, Nolan 1978]; Red-winged Blackbird [*Agalaius phoeniceus*, Monnett and Rotterman 1980]). Conversely, in other species, mated pairs do not normally separate or move great distances after nest predation (e.g., European Blackbird [*Turdus merula*, Ribaut 1964]; Song Sparrow [*Melospiza melodia*, Tompa 1964]; Eurasian Skylark [*Alauda arvensis*, Delius 1965]; and Scrub Jay [*Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1984]). However, there have been only a few studies that have attempted to confirm statistically that within-season dispersal after nest predation is farther or more frequent than within-season dispersal after a successful nesting attempt. Wunderle (1984) found that female Bananaquits (*Coer-*

[1] 3662 Kinter Hill Road, Edinboro, Pennsylvania 16412.
[2] Dept. of Biology, York Univ., North York, Ontario M3J 1P3, Canada.

eba flaveola) were less likely to abandon their territories and mates if they had a successful nest. On the other hand, Shields (1984) found that Barn Swallows (*Hirundo rustica*), that are colonial and reuse nests, were more likely to change nests if the first nest was successful. Jackson et al. (1989) found that Prairie Warblers were equally likely to leave their mate's territory after successful or unsuccessful nests. Monnett and Rotterdam (1980) correlated distances female Red-winged Blackbirds moved after nest predation to the size of home ranges of predators.

In addition to within-season dispersal, nest concealment could be a factor in predation avoidance. For open nesting birds, a new nest site could differ from the original site in variables such as height, visibility, and cover that affect nest concealment. In Pinyon Jays (*Gymnorhinus cyanocephalus*), Marzluff (1988) found that nest height following predation was significantly lower (nest more concealed) than the height of the nest that was depredated. He also found that the jays' second nests after successful first nests were not significantly more concealed.

In this study, we tested the hypothesis that within-season dispersal and nest-site modification (e.g., changes in nest concealment) occur in Hooded Warblers (*Wilsonia citrina*) as a result of predation of previous nests. Hooded Warblers make good subjects for examining the effects of predation on within-season dispersal and subsequent nest site selection since they are often double brooded and will renest as many as three times in a season. In a previous study on nest concealment in Hooded Warblers (Howlett and Stutchbury 1996), we performed a vegetation-removal experiment to test if nest concealment affected nest predation. Nests manipulated to be highly visible did not suffer higher predation than control nests that remained concealed. Therefore, based on our previous findings, we made the prediction that females that suffer nest predation will not make their subsequent nests more concealed. Based on the tactic of moving a nest away from the site of predation to avoid the immediate presence of predators, we made two additional predictions: (1) females that suffer nest predation will renest farther away from their original nest compared with females that do not suffer predation; and (2) renests after predation will have a greater chance of success than all first nests combined.

METHODS

We conducted fieldwork during May–August of 1992–1995 in conjunction with other ongoing studies of this breeding population of Hooded Warblers (Mark and Stutchbury 1994, Stutchbury et al. 1994, Stutchbury and Howlett 1995, Howlett and Stutchbury 1996, Neudorf 1996, Tarof 1996, Evans Ogden and Stutchbury 1997). The study site was a mixed forest of approximately 150 ha in northwestern Pennsylvania (41°46′N, 79°56′W). We marked grids every 50 m with flagging tape and aluminum markers on nearest trees. Territories were mapped on metric graph paper by observing border disputes, sighting banded

males, or observing individuals that responded to playbacks of male song. We banded adult warblers with uniquely color-coded bands and aluminum U.S. Fish and Wildlife bands.

Nests were located primarily by following vocalizing females during nest construction, egg laying, or early incubation. Their open cup nests are made of bark and fine grasses with a base of dead leaves and are placed 0.29–1.46 m above the ground in a shrub (Howlett and Stutchbury 1996). A nest was considered successful if at least one nestling was fledged.

Measurements of nest and vegetation characteristics were taken within three weeks of a nest becoming inactive. We measured distances between first and second nests with a 50-m tape. We also determined distances and exact compass directions from nests to nearest grid markers and mapped the nests on graph paper.

The nest-site characteristics of nest height, stem density, and overall visibility of nest were used as variables of nest concealment. Stem density and visibility of nest were measured within a circle with a 1-m radius (3-m^2 area) centered around the nest (see Petit et al. 1988). To quantify stem density, we counted stems (>3 mm diameter and >20 cm tall) at ground level within the circle and calculated the stems per square meter.

We determined visibility scores using methods similar to those of Holoway (1991). All visibility scoring was done by J.S.H. to ensure consistency. Estimates of the percentage of the nest that was visible were made to the nearest 20%. These estimates were taken 1 m from the nest at ground level, at nest height, and at 1.5 m above ground, and they were taken every 45° compass interval (eight points) around the circle. One estimate was made from directly over the nest at a height of 1.5 m. The overall visibility was calculated as the average of the 25 estimates (see Howlett and Stutchbury 1996).

Nests included in this study were pairs of first nests and subsequent renests. Nest site variables were measured during the 1992 and 1993 seasons primarily for another study on nest concealment (Howlett and Stutchbury 1996). Distances between nests were measured in 1994 and 1995 as well as in 1992 and 1993.

Nest predators common at the study site were Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), eastern chipmunks (*Tamias striatus*), red squirrels (*Tamiasciurus hudsonicus*), gray squirrels (*Sciurus carolinensis*), fox squirrels (*Sciurus niger*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), weasels (*Mustela spp.*), opossums (*Didelphis virginiana*), and black rat snakes (*Elaphe obsoleta*). There was little Brown-headed Cowbird (*Molothrus ater*) parasitism as a result of a cowbird control program (Stutchbury 1997).

RESULTS

All nest failures were due to predation. None of the females deserted a territory or mate to renest. The average distance from all first nests (N = 47) to their subsequent renests was 48 m (range of 4–160 m). However, contrary to our prediction, renesting Hooded Warblers that were previously successful moved significantly farther away from their original nest sites compared with females who suffered predation (Fig. 1; Mann-Whitney *U*-test, $U = 146.5$, $P < 0.01$).

The size of a territory and the location of the first nest with relation to territory boundaries could affect dispersal distance since there was no territory desertion. We, therefore, estimated territory sizes and nearest distances from first nests to territory boundaries. Territories (N = 47) ranged from 4000 m^2 to 25,000 m^2. The mean territory size (8800 m^2) of territories with successful first nests (N = 22) was not significantly dif-

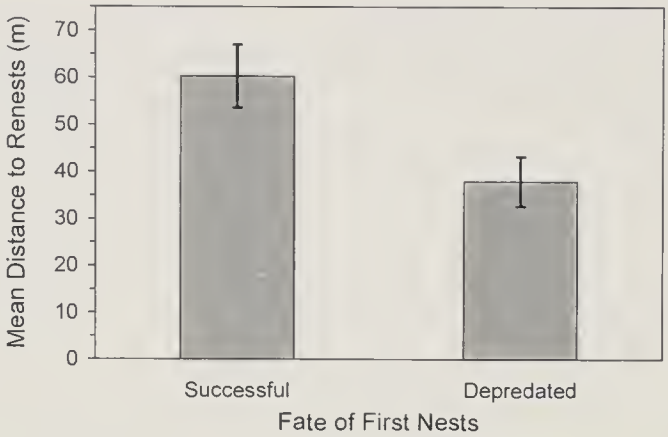

FIG. 1. Mean dispersal distances from successful (N = 22) and depredated (N = 25) first nests to subsequent renests. Error bars show ±SE.

ferent (Mann-Whitney *U*-test, $U = 266.0$, $P = 0.84$) from the mean territory size (8100 m^2) of territories with depredated first nests (N = 25). Also, the mean nearest distance to territory boundaries (19.2 m) for successful first nests (N = 22) was not significantly different (Mann-Whitney *U*-test, $U = 198.5$, $P = 0.10$) from the mean nearest distance (16.9 m) for depredated first nests (N = 25).

Each of the nest-site variables of concealment for all measured nests (N = 58) varied considerably (nest height, mean = 51.4 cm, range = 31.0–95.0 cm; stem density, mean = 24.3 stems-m^2, range = 4.1–58.0 stems-m^2; visibility overall, mean = 50.9%, range = 9.6–78.4%). Wilcoxon matched pairs tests clearly showed no significant differences between depredated nests (N = 19) and renests (Fig. 2; $Z = 0.65$–1.52, all $P > 0.05$). These variables also remained the same for successful nests (N = 10) and renests (Fig. 2; $Z = 1.17$–1.78, all $P > 0.05$).

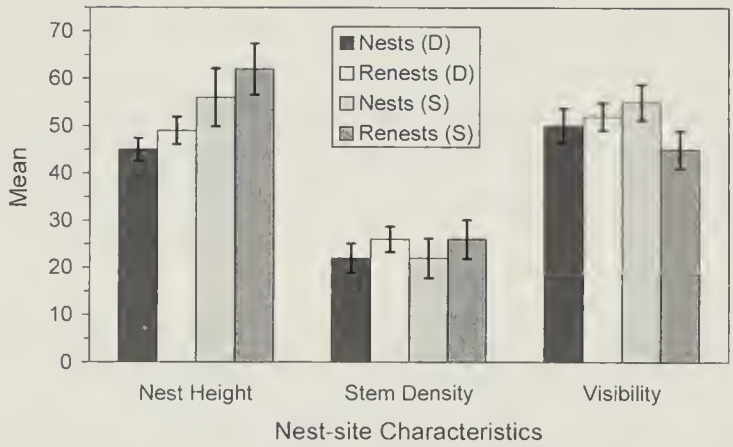

FIG. 2. Means of nest height (cm), stem density (stems-m^2), and overall visibility (% visible) for first nests and subsequent renests. On legend, (D) indicates depredated first nests (N = 19); (S) indicates successful first nests (N = 10). Error bars show ±SE.

The normal frequency of nest predation (all nests per year) of Hooded Warblers at our study site has been approximately 50% (Howlett and Stutchbury 1996). For nests included in this study, the frequency of predation was also 50% (49/98). The frequency of predation was 51% (25/49) for all first nests, 48% for renests following predation, and 50% for renests following successful first nests. Contrary to our prediction, a renest following predation was not more likely to be successful than a first nest (X^2 = 0.06, df = 1, P = 0.81), nor was a renest after a successful nest more likely to be successful than a first nest (X^2 = 0.01, df = 1, P = 0.93).

DISCUSSION

Our study examined the effects of nest predation in renesting Hooded Warblers. We expected nest predation to result in within-season dispersal but not greater nest concealment. Opposite to our prediction, females from successful first nests dispersed farther for their second nests than did unsuccessful females. We found no relationship between nest predation and subsequent nest concealment. In addition, renests after predation were no more successful than all first nests.

Why did successful females move their renests significantly farther away compared to females that suffered predation? An alternative hypothesis to explain within-season dispersal could be that this movement could be used by one member of the pair to terminate care of the fledglings, thus improving the probability of raising a subsequent brood elsewhere (Jackson et al. 1989). Indeed, female Hooded Warblers that have successful first nests usually help feed the fledglings with the male only until they begin incubating their second brood (Evans Ogden and Stutchbury 1997). The first egg date for the second clutch is often within a week of the first brood fledging date when the fledglings are still near their nest. Thus, females may be actively avoiding their fledglings in order to improve their success in renesting.

The avoidance of fledglings could serve to isolate a renest from fledgling activities that might attract predators. It could also serve to reduce competition for food resources. In support of the idea of reduced competition for food, Greig-Smith (1982) found that local food depletion was a factor in within-season dispersal of Stonechats (*Saxicola torquata*) and that nestling growth in second broods was better in nests that were at the greatest distances from previously successful nests.

Why do females not disperse or better conceal their nests in response to nest predation? One explanation could be that in Hooded Warblers nest-site selection is instinctual or based on imprinting on characteristics of the natal nest (Sargeant 1965, Cink 1976) and not affected by learning

from recent experiences. Another explanation could be related to the fact that females rarely desert their territories or mates to renest. From 1991 to 1995 we observed approximately 184 pairs of Hooded Warblers. We noted only 3 cases of territorial desertion by females (<2%). When females limit renesting to within the same territories, the area of the territories may not be large enough to avoid previous predators.

A third explanation could be that nest predation occurs by chance, regardless of placement or variations in characteristics of specific nest sites. When variations in nest-site characteristics are not factors in predation, they should also not be important factors in nest-site selection after predation. In this study, we found that depredated nest sites were no different from successful nest sites (Fig. 2) and that all nests and renests had about a 50% chance of success. Indeed, nest predation in Hooded Warblers at our study site appears to be random no matter the degree of nest concealment, the location of the nest, the age and plumage of the female, or the time of year (see Stutchbury and Howlett 1995 and Howlett and Stutchbury 1996).

In conclusion, we found that predation did not cause female Hooded Warblers to disperse or alter nest-site selection. Other variables may be more important in determining the location of renesting sites, such as the presence of fledglings and the availability of food resources, in the case of a successful first nest. We recommend that the predation-avoidance hypothesis be tested further on other species and in other habitats.

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BREEDING BIOLOGY OF ROYAL AND CAYENNE TERNS AT A MIXED-SPECIES COLONY IN PATAGONIA

FLAVIO QUINTANA[1] AND PABLO YORIO[1,2]

ABSTRACT.—We studied the breeding biology of Royal (*Sterna maxima*) and Cayenne terns (*S. eurygnatha*) at Punta León, Patagonia, during 1989–93. In all years, both species bred in a single colony with their nests intermingled. Colony size varied between 1,150 and 1,830 pairs. Colony formation occurred during the first or second week of October. Nesting densities were relatively high (9.8 to 11.1 nests/m^2). Both species started to lay eggs during the second and third week of October in all years. During 1993, clutch size for Royal and Cayenne terns was 1.3 ± 0.5 and 1.1 ± 0.3, respectively. The length of the incubation period was 25.7 ± 0.9 and 29.1 ± 3 days for Royal and Cayenne terns, respectively. During 1993, hatching success was 0.72 ± 0.34 and 0.68 ± 0.42 chicks per nest for Royal and Cayenne terns, respectively. Egg losses (45.3%) were mainly from predation. First-hatched chicks were observed during mid November. Chick survival to 10 days of age was 90% and 66.7% for Royal and Cayenne terns, respectively. At approximately 20 days of age, some tern chicks started to abandon the colony to form creches at the beach. Royal and Cayenne terns generally fed out of sight from the colony and preyed upon the same species, including *Odontestes* spp., *Stromateus brasiliensis*, *Engraulis anchoita*, and *Sprattus fuegnensis*. *Received 16 Jan. 1997, accepted 3 June 1997.*

Royal (*Sterna maxima*) and Cayenne (*S. eurygnatha*) terns are two widely distributed species. Royal Terns breed from eastern North America to Patagonia (Escalante 1985, Yorio and Harris, in press) while Cayenne Terns, considered by some authors as a race or color morph of the Sandwich Tern (*S. sandvicensis*) (Buckley and Buckley 1984, Gochfeld et al. 1994), breed from the southern Caribbean to Patagonia (Olsen and Larsson 1995, Yorio and Harris, in press).

In Argentina, both species breed at a few locations on the Patagonian coast (Zapata 1965, Korschenewski 1969, Daciuk 1972, 1976, Yorio et al. 1994). As in other regions (Bent 1921, Ansingh et al. 1960, Buckley and Buckley 1972a, Blus et al. 1979, Antas 1991), Patagonian Royal and Cayenne terns nest with each other or in association with other tern species (Zapata 1965, Daciuk 1973, Yorio and Harris, in press). On occasion, Royal and Cayenne terns breed in a single colony with their nests intermingled (Korschenewski 1969, Yorio et al. 1994).

Like other species of the crested tern group, Royal and Cayenne terns have natural history traits distinguishing them from other tern species. In

[1] Centro Nacional Patagónico, CONICET, Blvd. Brown s/n 9120, Puerto Madryn, Chubut, Argentina.
[2] Wildlife Conservation Society, New York, New York 10460.

general, crested terns breed at relatively high densities, frequently change colony site location, and do not remove egg shells from the nest. They do not disperse droppings, they sit tightly on the nest when approached by predators, their chicks are precocial leaving the nest soon after hatching to form creches, and breeders readily desert the colony when disturbed (Ansingh et al. 1960, Cullen 1960, Buckley and Buckley 1972a, Langham and Hulsman 1986). These traits appear to be anti-predator adaptations (Cullen 1960).

Royal and Cayenne tern breeding biology has been described at only a few locations in the United States (Kale et al. 1965, Buckley and Buckley 1972a, Blus et al. 1979) and the Caribbean (Ansingh et al. 1960). Other studies have described some aspects of their taxonomy (Junge and Voous 1955, Voous 1968, Buckley and Buckley 1984, Escalante 1984), distribution (Voous 1963, Ffrench and Collins 1965, Sick and Leao 1965, Zapata 1965, Buckley and Buckley 1984, Escalante 1991), feeding ecology (Buckley and Buckley 1974, Erwin 1977, 1978), and behavior (Ashmole and Tovar 1968, Buckley and Buckley 1970, 1972b, 1977, Grant 1981, Kilham 1981). Conservation problems of these species have been discussed by Daciuk (1973), Escalante (1982, 1985), Antas (1991) and Gochfeld et al. (1994). In the present paper, we describe the breeding biology of Royal and Cayenne terns at the Punta León mixed-species colony and compare our results with those of studies at other locations.

METHODS

Punta León (43°04′S, 64°29′W) is 10 km south of the mouth of Golfo Nuevo, Patagonia. The coast in this area is characterized by extensive cliffs 30–100 m high and gravel beaches along the shoreline. About 700 m of shoreline are separated from the cliffs by a silt platform of approximately 5 ha, covered by vegetation consisting mainly of *Suaeda divaricata, Atriplex lampa*, and *Lycium chilense*, and is used as nesting substrate by several seabird species. Seabirds breeding with Royal and Cayenne terns include Kelp Gulls (*Larus dominicanus*), Imperial Cormorants (*Phalacrocorax atriceps*, with both "atriceps" and "albiventer" color morphs), Olivaceous Cormorants (*P. olivaceus*), Rock Shags (*P. magellanicus*), and Guanay Cormorants (*P. bougainvillii*) (Malacalza 1987, Yorio et al. 1994).

To analyze the variation in numbers of both tern species within each season, we made weekly censuses throughout the 1989–1992 breeding seasons. We made counts with spotting scopes 20–45× from an observation point located on cliffs at a distance of 50–70 m from the colony. Early in the season when colony size was small, we obtained numbers by direct count of birds. Later in the season, we estimated the number of birds within a small area and extrapolated that count to the total colony area. We calculated the proportion of breeding pairs of each tern species by counting their nests along 10–30 imaginary transects covering the whole colony.

We estimated population size of both tern species from aerial photographs taken during peak egg laying (21 Nov. 1989, 7 Nov. 1990, and 15 Nov. 1993). We used a Cessna 182, flying at an altitude of 100–300 m, and took photographs with 80–200 and 300 mm lenses. We obtained total numbers of breeding pairs through counts by the two of us from projected

slides. We considered as "breeding pairs" all birds sitting as if they were incubating, birds standing on a scrape, and pairs of birds standing either within or at the periphery of the colony.

We calculated nesting densities after the breeding season was over by randomly sampling 1 m^2 quadrats within the colony. All nests with more than half of the nest cup within the quadrat were included in the count. We analyzed the distribution of nests using the Clark and Evans test (Rabinovich 1980). During all seasons, we obtained information on habitat characteristics from the observation points on the cliff.

Both terns are highly sensitive to human disturbance (Buckley and Buckley 1972a, Daciuk 1972, 1973, Escalante 1985, Antas 1991). Therefore, we obtained information through observations from the cliffs (1989–1993), from a blind (1993), and through automatic video recordings (1992–1993). During each season, we gathered data on colony formation, egg-laying and chick hatching dates, colony abandonment by adult birds and chicks, and creche formation on the beach from cliff observations.

During 1992 and 1993, we monitored 27 and 58 nests, respectively, of both tern species using an automatic video camera located at the periphery of the colony. Recordings were made at regular intervals through daylight hours from settlement to hatching. During 1993, we also identified and monitored 36 Royal Tern and 28 Cayenne Tern nests from a mobile blind located 1–2 m from the tern colony. We previously tested the effects of the mobile blind by making gradual approaches to the nesting birds, never observing nest abandonment. Using maps, we identified all study nests every two days and recorded adult presence, stage of the breeding cycle, and number of eggs or chicks. We categorized nests by species (Royal or Cayenne) and location within the colony (central or peripheral). We defined as peripheral any nest that was not completely surrounded by other tern nests. These were generally located in the first or second row from the edge of the colony.

We estimated egg losses from predation by assuming that disappeared eggs had been preyed upon. We estimated chick survival to the first ten days of age, as approximately at that age chicks start to move within the colony and individuals cannot be followed if unmarked. We did not mark chicks to avoid disturbance and, therefore, we could not obtain information on chick survival after 10 days.

During 1992 and 1993, we obtained information on the prey captured by both tern species during the chick stage through observation of adults arriving with food at the colony. Like other terns, both species at Punta León bring food back to the colony carrying only one prey item in the beak per trip. We identified prey species through direct observation from the blind and cliff using binoculars and spotting scopes.

RESULTS

Royal and Cayenne terns started to arrive at Punta León in mid-September and remained courting and mating on the beach for up to a month before finally settling in the colony site. Between arrival at Punta León and final settlement in the colony, terns stayed in the area for only a few hours a day, but during the evenings there was an increase in the number of individuals.

At Punta León, courtship and copulation behaviors occurred mainly on the beach and were similar for both species. Behaviors observed consisted of terrestrial and aerial displays, both including courtship feeding. Courtship behavior of both tern species was similar to that described elsewhere

for these species (Buckley and Buckley 1972a, Kilham 1981) and for other crested terns (Cullen 1960, Smith 1975).

During all seasons, settlement at the colony site occurred during the second or third week of October. Colony formation was always initiated by a group of about 100–150 Royal Terns and the colony grew through the gradual settlement of new groups of both species at the periphery. As a result, both species bred in a single colony with their nests intermingled. During all years, Cayenne Terns started nesting after the first group of Royal Terns started laying eggs. Nesting rate for both species was lower in 1991 than in previous years (Fig. 1). The number of terns at the colony increased rapidly during the second and third week of October and reached a maximum during the first or second week of November, depending on the breeding season (Fig. 1). Colony size varied among seasons (Table 1).

In all seasons, the colony was located 10–20 m from the high tide line and approximately 1m above sea level. Nests were located in sections of bare ground surrounded by *S. divaricata* bushes up to 1.5 m tall. In all years, the colony was located within the Kelp Gull colony, and therefore was always surrounded by gull nests. Kelp Gulls start nesting more than a month before Royal and Cayenne terns (Yorio et al. 1994) and nests both on bare ground and under vegetation (Yorio et al., in press). The location of the colony was variable between years. Royal and Cayenne terns settled during the first three years close to the north end of the cormorant colony, but during 1991 they moved approximately 150 m to the south to another section of the Kelp Gull colony, where they nested up to 1994.

Tern nests consisted only of a scrape on the bare ground, made with their feet while sitting. Nests were evenly distributed throughout the open space and packed close together, showing hexagonal packing similar to that described by Buckley and Buckley (1977). Nests had a homogeneous distribution (Clark and Evans test, $r = 33.2$). Nesting densities were relatively high (Table 2), and the average distance between adjacent nests was 29.8 ± 2.6 cm (N = 29) for 1989 and 31.4 ± 2.4 cm (N = 40) for 1992.

First eggs were laid between the second and third week of October in all years. Most pairs laid their eggs on the same day that they settled in the colony site. No significant differences were found between the clutch sizes of Royal and Cayenne terns (Mann-Whitney Test, 1992: $U = 32.5$, $P > 0.1$; 1993: $U = 178.5$, $P > 0.1$; Table 3).

During all years, pairs reused nest sites that had been used and abandoned by individuals of the same or the other species. For example, 28% of Royal Tern nests studied during 1993 (N = 36) were reused by Cay-

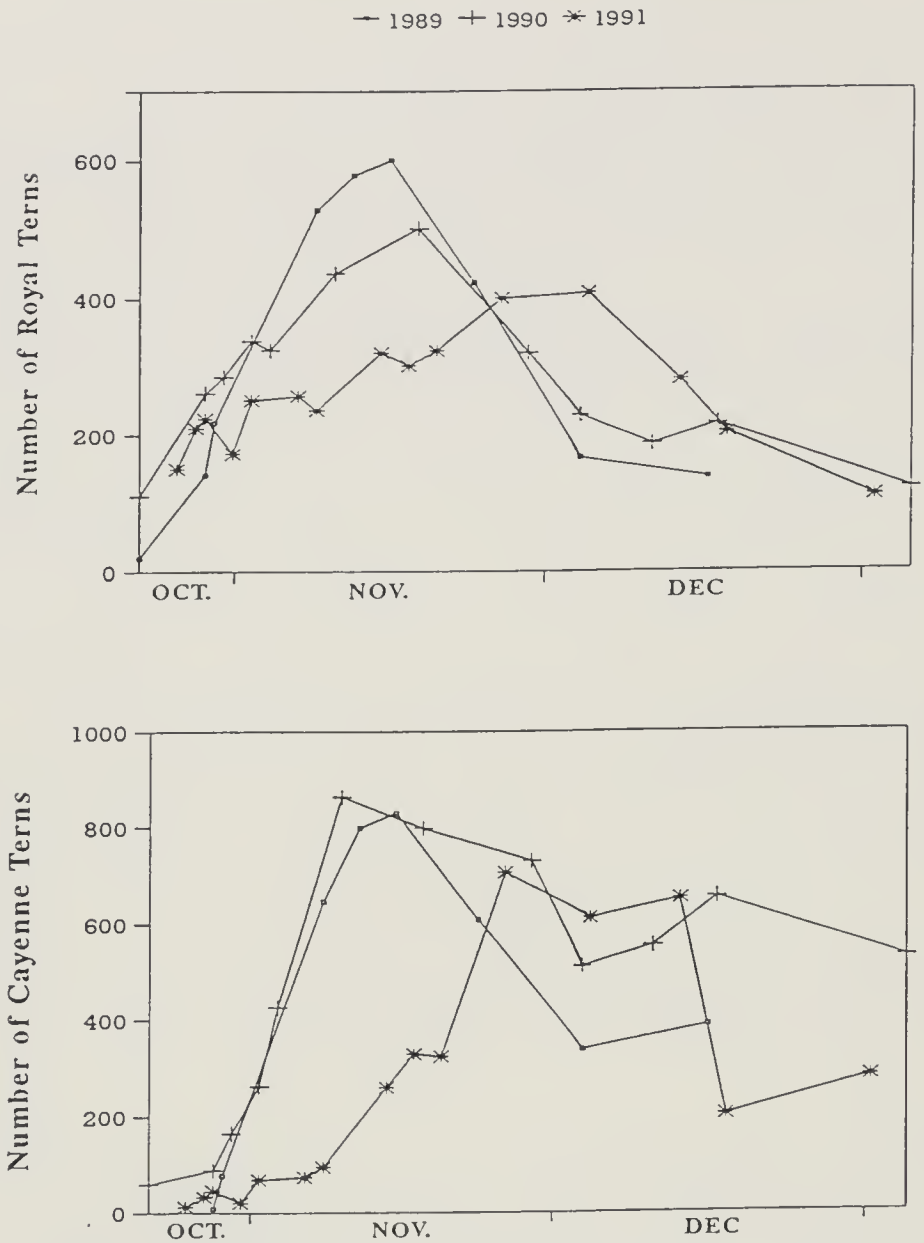

FIG. 1. Number of Royal and Cayenne terns as a function of time within the 1989–91 reproductive seasons.

enne Terns and 11% of Cayenne Tern nests (N = 28) were reused by Royal Terns.

The length of the incubation period (monitored daily from egg laying to egg hatching using the video camera) was 25.7 ± 0.9 days (N = 6) for Royal Terns and 29.1 ± 3.0 days (N = 25) for Cayenne Terns. Similarly, the length of the incubation period for 16 Royal Tern nests that were monitored from the blind was between 25 and 28 days. In all cases, the incubation period was similar to that observed for the same species

TABLE 1

NUMBER OF BREEDING PAIRS OF ROYAL AND CAYENNE TERNS AT PUNTA LEÓN DURING THE 1989, 1990, AND 1993 BREEDING SEASONS

Year	Number of breeding pairs		
	Royal Tern	Cayenne Tern	Total
1989	497	656	1153
1990	687	1140	1827
1993	—	—	1565

at other locations (Ansingh et al. 1960, Buckley and Buckley 1972a, Blus et al. 1979).

Hatching success was similar for both tern species (Mann-Whitney Test, 1992: $U = 46.5$, $P > 0.1$; 1993: $U = 218.5$, $P > 0.1$; Table 3). Of 64 Royal and Cayenne tern nests studied from the blind during 1993, 45.3% were preyed upon. All nests that lost eggs from predation were peripheral. Eggs disappeared from 78.4% (N = 37) of the peripheral nests. Kelp Gulls are the main predator of tern eggs at Punta León (Yorio and Quintana, in press). Nest desertion was low, as only one pair of each species deserted their nest during the incubation period. Heavy rains were also a cause of egg losses at the Punta León colony during 1993 when at least 30 pairs of both tern species, not included in the study sample, lost their eggs because of nest flooding. However, heavy rains are infrequent in the study area.

First-hatched chicks were observed during the first and second week of November, except in 1991, when they started hatching during the third week of November. During the first few days after hatching, chicks of both species remained at the nest, mostly under their parents. At three or four days of age, chicks started to move up to 0.5 m away from their nest. Of 20 Royal Tern chicks hatched in 1993, 90% survived up to 10

TABLE 2

NESTING DENSITIES FOR ROYAL AND CAYENNE TERNS AT PUNTA LEÓN DURING THE 1989 TO 1992 BREEDING SEASONS (N = NUMBER OF QUADRATS)

Year	Nesting density (nests/m^2)
1989	11.1 ± 1.25 (N = 20)
1990	11.1 ± 1.39 (N = 26)
1991	9.8 ± 1.21 (N = 29)
1992	10.0 ± 1.50 (N = 29)

TABLE 3
CLUTCH SIZE AND HATCHING SUCCESS OF ROYAL AND CAYENNE TERNS DURING 1992 AND 1993 AT PUNTA LEÓN

	Percentage of nests		Clutch size (Mean ± SD)	Hatching success (Mean ± SD)	Number of monitored nests
	1 egg	2 eggs			
1992					
Royal Tern	59	41	1.4 ± 0.5	0.79 ± 0.24	22
Cayenne Tern	100	0	1.0 ± 0.0	0.60 ± 0.49	5
1993					
Royal Tern	67	33	1.3 ± 0.5	0.72 ± 0.34	9
Cayenne Tern	86	14	1.1 ± 0.3	0.68 ± 0.42	49

days of age, while of six Cayenne Tern chicks, 66.7% survived to that age.

At least one parent remained attending the nest until chicks were approximately 20 days of age. At that age, some tern chicks abandoned the colony to form creches at the beach. Other chicks remained alone or in groups within the colony or started to form groups at the colony periphery. These chicks remained at the colony for more than a month before moving to the beach. The first mixed-species creches were always observed in early December, and chick groups at the beach were highly mobile.

Royal and Cayenne terns generally fed out of sight at the observation point at the cliff. When observed foraging within 500 m from the colony, they did it alone or in groups of 5–20 individuals. Royal and Cayenne terns preyed upon the same food species (Fig. 2). These included silversides (*Odontestes* spp., Fam. Atherinidae), juvenile butterfish (*Stromateus brasiliensis*; Fam. Stromateidae), Argentine anchovy (*Engraulis anchoita*; Fam. Engraulidae), and Fueguian sprat (*Sprattus fueguensis*; Fam. Clupeidae). On only one occasion did we see a Royal tern carrying Argentine red shrimp (*Pleoticus muelleri*; Fam. Solenoceridae).

DISCUSSION

In all seasons, nesting started with a group of Royal Terns, around which the colony expanded gradually and continuously through the establishment of groups of both species at some sectors of the colony periphery. Site occupation by dense groups of birds has been previously reported for Sandwich Terns (Taverner 1970, Veen 1977) and Elegant Terns (Barrie 1975, Villa Ramirez 1976), and it is argued that it could be an important factor determining the outcome of interspecific competition

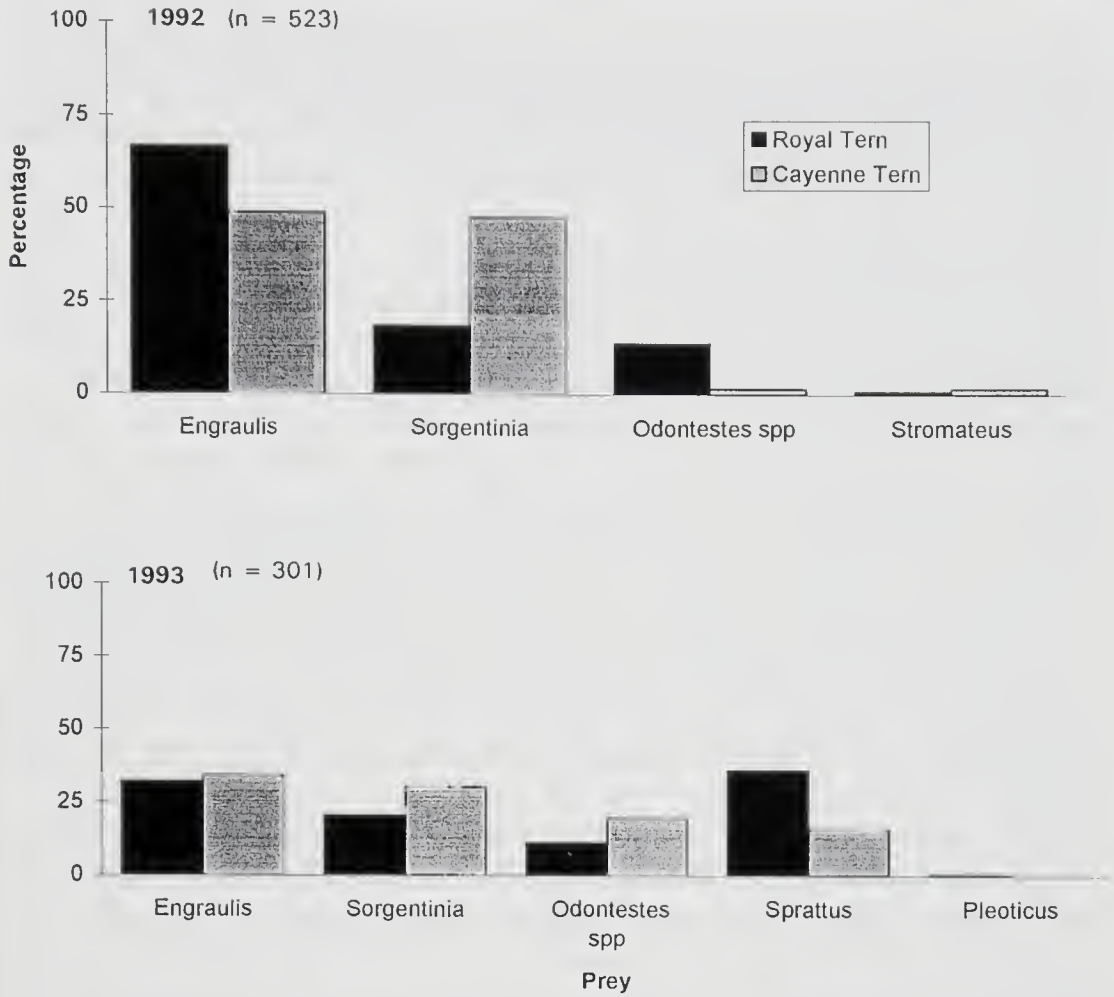

FIG. 2. Percentage of occurrence of prey types brought to the Punta León colony by Royal and Cayenne terns during the early chick stage in 1992 and 1993.

for nest sites (Burger 1985). At Punta León, this nesting behavior allows both tern species to displace already nesting Kelp Gulls and, therefore, compete successfully for nest sites with this larger and earlier-nesting species (Quintana 1995). Royal and Cayenne terns bred every year within the Kelp Gull colony. Terns might be gaining a protective advantage by moving into the gull colony if the access of potential predators were prevented by gull territorial behavior (Yorio and Quintana, in press).

In all years, Royal and Cayenne terns nested at relatively high densities, a common trait of the crested tern group (Cullen 1960, Ansingh et al. 1960, Buckley and Buckley 1972a, Langham and Hulsman 1986). At Punta León, nest densities were higher than those found in other crested terns (Langham 1974, Langham and Hulsman 1986), and previously reported in Royal Terns (7.4 nests/m^2, Buckley and Buckley 1972a), but lower than those observed at colonies where Cayenne Terns nest in mono-

specific clusters (12–13 nests/m^2, Ansingh et al. 1960). Royal Terns are larger than Cayenne Terns (Olsen and Larsson 1995) which could explain the intermediate nest densities found in the mixed-species colony at Punta León when compared to monospecific clusters of each species at other locations.

Nesting at high densities has been frequently cited as one of the main adaptive advantages of coloniality, as it reduces predation (Wittenberger and Hunt 1985). Buckley and Buckley (1972a, 1977) concluded that high nesting densities in Royal Terns have evolved as a result of low availability of nesting space and extreme egg predation by gulls on the periphery of the colony. At Punta León, egg predation by Kelp Gulls is the main factor affecting tern breeding success (Yorio and Quintana, in press), and predation occurred mainly on peripheral nests. High-nesting densities of Royal and Cayenne terns at Punta León appear to be an important factor in decreasing predation on central nests by aerial predators (Yorio and Quintana, in press). Similar findings have been reported for other crested terns, where peripheral nests were more suceptible to predation by gulls than central nests (Buckley and Buckley 1972a, Langham and Hulsman 1986).

Early formation of chick groups and colony abandonment, a trait found in the crested tern group, was also observed at Punta León. However, chicks started grouping and leaving the colony after they were more than three weeks of age, significantly later than was observed for Royal and Cayenne terns in previous studies (Ansingh et al. 1960, Buckley and Buckley 1972a). Those studies indicated that the formation of chick groups within the colony and colony abandonment occur a few days after hatching, similar to the Sandwich Tern (Cullen 1960, Smith 1975) and Crested Tern (*Sterna bergii*) (Langham and Hulsman 1986). The differences found in the timing of colony abandonment and creching by chicks could be due to a different degree of disturbance between the studies. Smith (1975), for example, found that colony abandonment was earlier in colonies of Sandwich Terns subject to human disturbance. Several studies on crested terns describe the high mobility chicks show in response to investigator approaches, while the study at Punta León was conducted without entering the colony, thus minimizing the disturbance.

Both tern species at Punta León fed mainly out of sight of the coast and captured the same prey species. For both terns, diet was similar in both study seasons, except for the presence of the Fueguian sprat in 1993. Fueguian sprat are not regularly found in the study area and are only occasionally recorded as a result of the intrusion of cold water currents from the south (G. Caille, Universidad Nacional de la Patagonia, pers. comm.).

One of the main features of the Punta León colony is the close association between species during nesting. Royal and Cayenne terns breed in a single group with their nests intermingled and at relatively high densities. This type of mixed-species colony has not been described for other tern species and has only been reported by Korschenewski (1969) for Royal and Cayenne terns breeding at Punta Tombo, Chubut, Argentina. Both species have been previously described as breeding in discrete groups within less dense colonies of other species such as South American Terns (*S. hirundinacea*) and Common Terns (*S. hirundo*) (Bent 1921, Ansingh et al. 1960, Buckley and Buckley 1972a, Daciuk 1973, Blus et al. 1979, Antas 1991).

The nesting association between Royal and Cayenne terns also occurs at other coastal locations in Patagonia, such as southern Buenos Aires, southern Chubut, and northern Santa Cruz (Pérez et al. 1995, Yorio and Harris, in press). This nesting association appears to be possible because of the similar breeding strategies of both tern species. Our results show that both terns have a wide overlap in habitat requirements and timing of breeding and, apparently, feed on the same prey species. The reasons why both species associate in this way during breeding are not clear, although it might be advantageous for Royal and Cayenne terns to nest together to reduce predation. Given the high density of the mixed-species tern colony, it is difficult for avian predators to steal eggs from central nests, leaving only peripheral nests vulnerable to predation. Therefore, an increase in the size of the colony as a result of the mixed nesting of both species would be advantageous as it reduces the number of exposed nests in relation to total colony size.

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VOCALIZATIONS, BEHAVIOR AND DISTRIBUTION OF THE RIO BRANCO ANTBIRD

KEVIN J. ZIMMER,[1] ANDREW WHITTAKER,[2] AND DOUGLAS F. STOTZ[3]

ABSTRACT.—We here present the first detailed analysis and sonagrams of the vocalizations of the Rio Branco Antbird (*Cercomacra carbonaria*) and augment the scant literature concerning its abundance, habitat preferences, and behavior. Based on vocal similarities, we examine the possible relationships of the Rio Branco Antbird to other species in the genus.
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As currently recognized, the genus *Cercomacra* consists of 12 species (Sibley and Monroe 1993, Bierregaard et al. 1997, Graves 1997) of medium-sized antbirds. The genus is poorly known, as evidenced by the discovery of two new species of *Cercomacra* and the elevation of another subspecies to species in the last decade (Fitzpatrick and Willard 1990, Bierregaard et al 1997, Graves 1997). Fitzpatrick and Willard (1990) proposed that the genus contains two distinct species groups, with one species (*C. cinerascens*) intermediate. They labelled these two groups the "*nigricans*-group" (consisting of the species *C. nigricans*, *manu*, *melanaria*, *ferdinandi*, and *carbonaria*) and the "*tyrannina*-group" (then consisting of the species *C. tyrannina*, *serva*, *nigrescens*, and *brasiliana*) (Fitzpatrick and Willard 1990). A subsequent cladistic analysis of plumage and vocal characters of the "*nigricans*-group" by Silva (1992) supported the hypothesis that the group is monophyletic and that *C. cinerascens* is the sister taxon of all five included species but reached different conclusions from Fitzpatrick and Willard concerning the phylogenetic relationships of species within the complex.

The Jet Antbird (*C. nigricans*) is the most widely distributed species of the *nigricans*-group as defined by Fitzpatrick and Willard (1990), occurring both east and west of the Andes from Panama to western Ecuador and northeastern Venezuela (Ridgely and Tudor 1994). The recently described Manu Antbird (*C. manu*; Fitzpatrick and Willard 1990) is now known to be widely, but apparently locally, distributed south of the Amazon from southeastern Peru to east of the upper Rio Tapajós, Mato Grosso, Brazil (Parker et al. in press, Zimmer et al. in press). The remaining three species have limited distributions around the perimeter of the Amazon Basin (mapped in

[1] 1665 Garcia Rd., Atascadero, California 93422.
[2] Estrado do Aleixo, con Junto Acariquara Sul, Rua da Samau'mas 214, Manaus, Brazil 69085.
[3] Environmental and Conservation Programs, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Drive, Chicago, Illinois 60605.

Fitzpatrick and Willard 1990). The Mato Grosso Antbird (*Cercomacra melanaria*) is found in northern and eastern Bolivia, southwestern Brazil in Mato Grosso and Mato Grosso do Sul, and in extreme northern Paraguay (Ridgely and Tudor 1994). The ranges of *C. carbonaria* (extreme northern Brazil along the Rio Branco and some major tributaries) and Bananal Antbird (*C. ferdinandi*) (largely Bananal Island in the Araguaia-Tocantins drainage) are among the smallest of all South American birds, and consequently, little is known of their vocalizations or natural histories.

In this paper we present the first published behavioral accounts and vocal analysis of *C. carbonaria*, the Rio Branco Antbird, and comment on its possible relationships to other species in the group, as suggested by vocal comparisons. We also attempt to determine why its distribution is so small.

STUDY AREA AND METHODS

Zimmer and Whittaker observed Rio Branco Antbirds between 1–3 Nov. 1994 along an approximately 10-km transect of the Rio Branco, from the city of Boa Vista, Roraima, Brazil, to just north of Ilha São Jose (ca 2°53′N, 60°33′W; Fig. 1). Whenever individuals or pairs of *C. carbonaria* were located, we followed them for as long as possible, summarizing foraging and other behaviors on cassette tape. Tape-playback was used to assess presence or absence of Rio Branco Antbirds in places where no spontaneously vocalizing birds were heard, and also to determine limits of territorial boundaries. All measurements included in such summaries (height above ground, territory size, distances, etc.) are estimates. Terminology for foraging behaviors follows Remsen and Robinson (1990). Two additional foraging terms used here are "hitching" and "side-to-side hitching." As used in this paper, "hitching" is a slight modification of the term as used by Whitney and Pacheco (1994) and is defined as movement in which both feet are moved sideways either simultaneously or in rapid succession, such that the axis of the body is held at an obvious angle (if not perpendicular) to the substrate (stem, vine, branch, etc.) and progression is made by a series of short advances. "Side-to-side" indicates hitching progression in which the orientation of the body relative to the substrate changes from one motion to the next, such that the bird leads first with one side, then with the other. We have also included observations made by Stotz 13–16 Oct. 1987 and Feb.–March 1992 on the distribution, abundance, and habitat of Rio Branco Antbirds near Boa Vista.

We recorded songs using Sony TCM-5000 recorders and Sennheiser MKH-70 and ME-80 microphones. All recordings by Zimmer have been or will be archived at the Library of Natural Sounds, Cornell Univ., Ithaca, New York. We made sonagrams on a Macintosh Centris 650 computer using Canary version 1.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York), Canvas version 3.0.6 graphics software (Deneba Software, Miami, Florida), and a LaserWriter Pro 630 printer. We examined specimens of all species in the *nigricans* group, as well as *C. cinerascens*, at the Field Museum of Natural History (FMNH) and at the Los Angeles County Museum of Natural History (LACM). Neither instituition has female specimens of *C. ferdinandi* or *C. melanaria*.

RESULTS

Cercomacra carbonaria is limited to the middle sections of the Rio Branco and its tributaries, in Roraima, extreme northern Brazil, and ad-

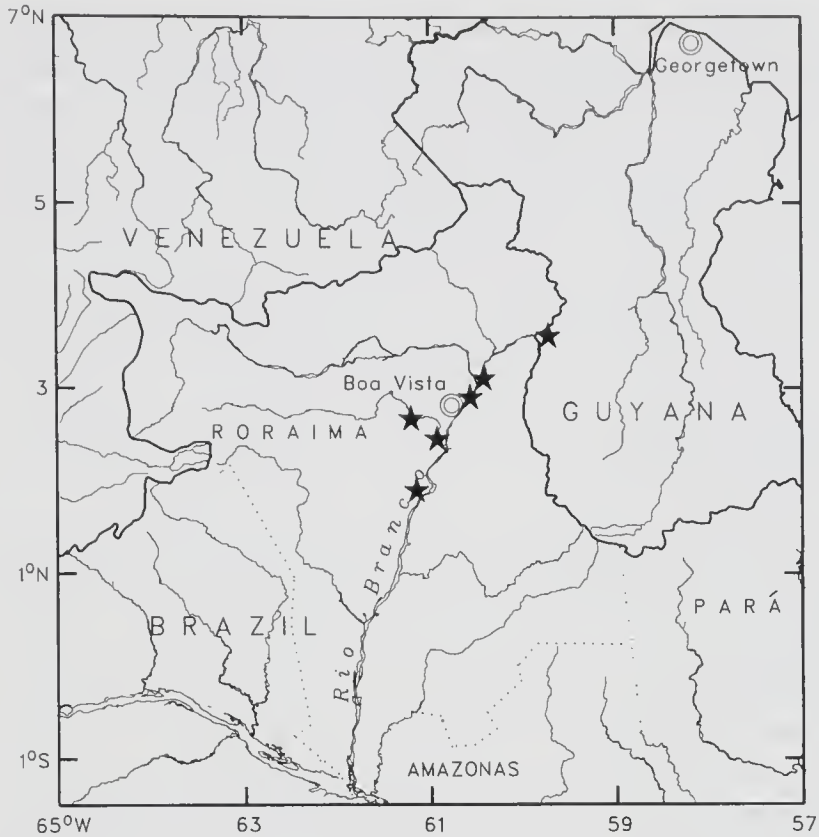


FIG 1. Distribution of Rio Branco Antbird (*Cercomacra carbonaria*): black stars indicate sites where specimens have been collected (all localities from Collar et al. 1992), or where the presence of Rio Branco Antbird has been documented by tape recordings (Guyana records from D. Finch recordings, LNS). The black star located immediately north of Boa Vista coincides with the sites at which the authors studied *C. carbonaria*.

jacent Guyana. It ranges from Caracarai in the south (Fitzpatrick and Willard 1990) north along the Rio Branco and Rio Tacutu to the Ireng River (Rupuruni District), Guyana, less than 2 km from its confluence with the Tacutu (D. Finch, pers. commun.). It has also been found on the Rio Mucajaí, a tributary of the Branco (Collar et al. 1992). In October 1987, Stotz found *C. carbonaria* at five sites near Boa Vista—the east bank of the Rio Tacutu ca 2 km above its mouth, the east bank of the Rio Branco 15 km northeast of Boa Vista, the west bank of the Rio Branco 10 km northeast of Boa Vista, Ilha Boa Água (on the Rio Branco north of Boa Vista); and on Ilha São José on the Rio Branco ca 10 km north of Boa Vista (Collar et al. 1992). Stotz also visited the type locality, Fortaleza de São Joaquim (28 km above Boa Vista), but found the habitat greatly altered and saw no signs of *C. carbonaria*. At least 18 birds were seen or heard during the 1987 survey, and the species appeared to be fairly common. In February and March 1992, Stotz found at least five

males along about 3 km of thickets lining a dry braid of the Rio Branco at Fazenda Santa Cecilia (directly across the river from Boa Vista).

In November 1994, Zimmer and Whittaker found *C. carbonaria* north of Boa Vista, where its distribution was patchy, on the sides of the river, with only four scattered pairs on either bank of the Rio Branco (west bank opposite the north end of Ilha São José, west bank ca 300 m south of Ilha São José, east bank ca 1 and 2 km south of Ilha São José). North of Boa Vista the Rio Branco is lined by a narrow band of gallery forest mostly less than 150 m wide. Beyond the immediate vicinity of the river, the predominant vegetation is savanna dotted with patches of low-canopied savanna woodlands on white sand soils and extensive stands of buriti palms (*Mauritia flexuosa*) in the lower-lying areas.

Pairs of antbirds along the banks of the river inhabited dense thickets at the edge of the gallery forest, within 100 m of the river. Systematic tape playback (every 50–100 m) along 300–500 m of suitable habitat at many points along both banks of the river did not elicit a response. Antbirds were either vocalizing spontaneously or were strongly responsive to tape playback, namely an immediate vocal response and approach. When no further playback was forthcoming, many birds continued to sing for several minutes. At no time did these extended song periods produce a vocal response from other birds. Similarly, we surveyed ca 2 km of tall-canopy (20–30 m) várzea forest along the Parana do Sulhão (a small tributary of the Rio Branco a few kms north of Boa Vista) by boat, presenting tape playback at 100-m intervals, with no response. We also surveyed an extensive stand of savanna woodland (canopy height of 20+ m) on the right bank of the Rio Branco separated from the strip of gallery forest by ca 500 m of open savanna. No *C. carbonaria* were found there, nor at the edge of tall forest a few hundred meters from the left bank opposite Boa Vista. In 1987, Stotz found *C. carbonaria* away from islands only in dense thickets along the river edge. They did not occur in other forested or semi-forested habitats. Similarly, birds were found only in thickets along a seasonally dry braid of the Rio Branco during an intensive two-week survey of the Fazenda Santa Cecilia.

We found the Rio Branco Antbird to be common on Ilha São José, in a variety of habitats. In November 1994, individuals on the west side of the island were in dense second-growth (mostly in overgrown manioc plantations with widely scattered 20–30 m trees) similar to habitat favored by *C. nigrescens* south of the Amazon (pers. obs.). *Cercomacra carbonaria* seemed to be evenly distributed within this habitat, and at one point we located three calling pairs within 150 m of one another. On the east side of the island we located five pairs along ca 500–550 m of forest edge, with two more pairs heard calling distantly inside the forest. The

interior island forest was densely wooded, with a canopy of 20–30 m, and was bordered (at the southeast end of the island) by a uniform, ca 30 m wide band of a single species of tree (with leaf characteristics similar in appearance to *Inga* spp.) ca 8 m in height, with occasional overtopping *Cecropia* or other large trees. Although antbirds were seen foraging in this outer band of trees, and readily entered it in response to tape playback, they were spent most of their time in the floristically more diverse interior forest. The edge vegetation was used more in the first hour of the morning, when the birds were also most vocal.

Diameter of antbird territories, measured by walking along the sandbars bordering the forest edge and conducting playback trials, appeared to be no more than 100–150 m. We saw few interactions between males of adjacent pairs at territorial boundaries. None of these appeared to be particularly aggressive or sustained. Two males approached to within 1 m of one another, uttering staccato "kud-up" notes and subdued whiny sounds (see *Vocalizations*) while erecting their hindcrown feathers and exposing the normally hidden, white margins of the lesser coverts and the white interscapular feathers. This encounter did not result in any chase behavior, nor in a true song bout, and only one of the two males subsequently sang (and then only sporadically). Other interactions involved mutual approach to within 5–8 m, with one bird typically singing and the other remaining quiet and somewhat passive. The passive bird in such interactions frequently picked at bare branches seemingly devoid of prey, as if displacing aggression. Females responded to tape playback by vocalizing, but were generally more reluctant to approach than males. On one occasion we observed two pairs interacting at a territorial boundary. The two males approached to within 6 m of one another, and the respective females remained several meters farther back in the thickets. One male sang several songs, which elicited an excited duet from the other pair of birds. This was followed by closer mutual approach on the part of the males and some subdued aggression calls before both pairs retreated.

Apparent low density of Rio Branco Antbirds in seemingly suitable "mainland" habitats north of Boa Vista is puzzling, given the abundance of the species on Ilha São José. The discrepancy is particularly intriguing since antbirds on Ilha São José appear to be habitat generalists, occupying a variety of wooded and thicket habitats in high densities. Because our visit came well into the dry season, it is possible that failure to find *Cercomacra* reflected seasonal lack of territorial response rather than true scarcity. Few species were particularly vocal during our November visit, and several expected riverine species seemed to be curiously absent (=non-vocal). For most passerines, tape playbacks are most useful in eliciting a response early in the breeding season (pers. obs.). A drop-off

in song intensity between October and November could also account for the apparent higher densities of *Cercomacra* found by Stotz in 1987.

The distance between the known northern and southern range limits of *Cercomacra carbonaria* is about 210 km. Less than 20 km of the lower Rio Mucujaí has appropriate habitat (Stotz, pers. obs.). No Rio Branco Antbirds have been found along other main tributaries (such as the Rio Uracoeira) in the region (Stotz, pers. obs.). A maximum of 460 linear km of river edge, therefore, might be occupied by *Cercomacra carbonaria*. Suitable habitat within this belt is confined to within 0.5 km on either side of the river. Including the few (<10) river islands with significant vegetation between Boa Vista and the Rio Tacutu, this would give a total area potentially occupied by *Cercomacra carbonaria* as perhaps 250 km^2, or less. If densities of Rio Branco Antbirds on the mainland are estimated at one pair per 250 m of river edge (almost certainly greatly overestimated), and densities on the river islands are extrapolated from our estimates of territory size on Ilha São Jose, we would arrive at a maximum mainland population of 3700 birds, with perhaps another 500–1000 on river islands. These estimates are crude by any measure, but they do emphasize the tiny range and global population of *Cercomacra carbonaria*, as well as the linear nature of its habitat.

Molt and morphology.—In November 1994, several males were actively molting rectrices. A female collected by Stotz in October 1987 had small gonads and was in heavy molt (body, wings, and tail). This is consistent with singing patterns, and further suggests that the dry season is the non-breeding season for *Cercomacra carbonaria*. Soft-parts colors for both sexes were as follows: bill black; legs and feet gray; iris medium-brown.

Foraging behavior and sociality.—Rio Branco Antbirds were particularly difficult to follow, in part due to their secretive nature, and in part due to the nearly impenetrable nature of their preferred habitats. Both males and females flicked their wings frequently while foraging, and wagged their tails up and down in a shallow (ca 20°) arc, above and below the plane of the body. They generally traced a zigzag route through the foliage, progressing with several consecutive hops in a given direction before changing course. Hops carried the birds anywhere from 5 cm to 1 m at a time, and were separated by pauses of 0.5–2.0 seconds to peer about. Birds usually assumed a posture in which the body was held between horizontal and 45°. One male foraged from 1–7 m above the ground, but spent perhaps 75% of its time between 3.5 and 7 m above ground. It hitched rapidly along bare slender limbs without hitching from side-to-side. It picked three times at thin woody vines without visible success, and was seen to glean an unidentified arthropod from the underside of an overhanging green leaf by

stretching and reaching upward with a quick stab. Another male was seen to cling with its feet and reach downward to glean an unidentified medium-sized arthropod from the top surface of a green leaf 1 m above the ground in a shrubby forest border. This same male fluttered down suddenly from 2 m above ground to 1 m above ground to chase a flushed katydid. A pair of antbirds foraging within 5–7 m of one another gleaned a few small, unidentified arthropods from green leaves in the crowns of forest-edge trees ca 5–10 m above the ground.

Rio Branco Antbirds foraged individually or in pairs that remained in frequent vocal contact with one another. We did not find them associating with mixed-species flocks. Common insectivorous species found near *Cercomacra carbonaria* at all localities included *Picumnus spilogaster*, *Xiphorhynchus picus*, *Furnarius leucopus*, *Sakesphorus canadensis*, *Inezia subflava*, *Myiopagis gaimardii*, *Todirostrum maculatum*, *Thryothorus leucotis*, *Polioptila plumbea*, *Cyclarhis gujanensis*, and *Hylophilus pectoralis*.

Vocalizations.—We tape-recorded several different vocalizations from *C. carbonaria*. The primary, or territorial, song appeared to be a two-noted "hitch-COCK" repeated 4–10 times (most commonly 4–7 times) at the rate of about two couplets per second (Fig. 2A). This song was observed to be given only by males. When responding to tape playback, males increased the pace and sometimes lengthened the series of couplets, but otherwise sang identical songs.

Pairs engaged in duets (Fig. 2B) when responding to playback and when re-establishing contact during foraging. Such duets typically began with male two-noted songs, into which the female interjected (at any point in the male song) a loud, sharp "ECK" note. Typically, the female only "interrupted" 1–2 male song-couplets before the male switched from the two-note song to a single loud "OCK". Both birds then proceeded to deliver an antiphonal series of "ECK" (female) and "OCK" (male) notes in a rapid (3–4 combined notes per second) barking cadence that lasted 3–5 seconds. Thus, the introductory note of the female is not synchronized with the male, but it does lead to a synchronized duet. A peculiar feature of this duet is that the male always seemed to deliver the final note, often after a longer than average between-note interval.

In the few territorial interactions witnessed between two males, and in the single interaction witnessed between two pairs, birds of both sexes delivered a staccato "kud-up" or "kud-dudup" (Fig. 2C), often interspersed with single "kup" notes. Birds of both sexes also gave these aggression calls when they approached us closely following playback. A second contact call given both in territorial interactions as well as between mates when re-establishing contact following a separation, was a soft,

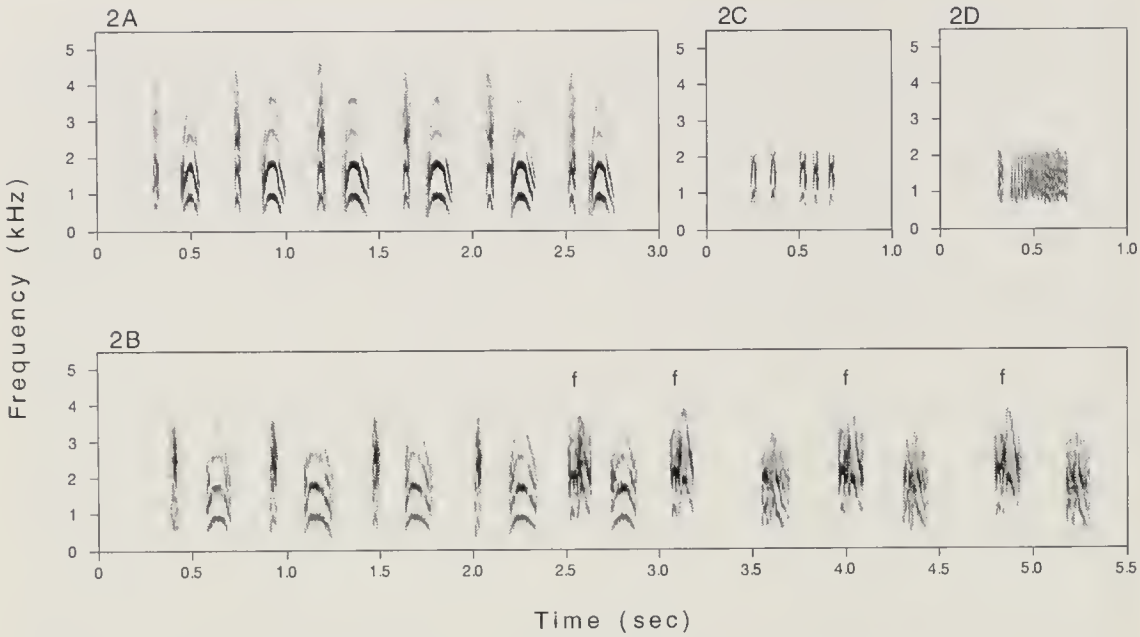


FIG. 2. Sonagrams of vocalizations of Rio Branco Antbirds, *Cercomacra carbonaria*: (A) male songs ("hitch-COCK'), (B) male song interrupted by single "ECK" notes of female and leading into male-female duet ("ECK-OCK"), (C) "kud-dup" and "kud-dudup" aggression calls of male (similar calls are also given by females), (D) "squeaking branch" contact call (this example delivered by a male, but similar calls are given by both sexes). All vocalizations recorded along the Rio Branco north of Boa Vista, Roraima, Brazil. All recordings by K. J. Zimmer.

whiny call that sounded like the subdued squeaking of a tree branch in the wind (Fig. 2D).

DISCUSSION

The two analyses of species relationships among the *C. nigricans* group (Fitzpatrick and Willard 1990, Silva 1992) have emphasized plumage pattern and color (especially females), and vocalizations. Fitzpatrick and Willard (1990) hypothesized that *C. manu* and *C. melanaria* were sister species, "possibly close enough to be recognized as a superspecies," based on extremely similar female plumages and narrower white tips to the rectrices in both sexes compared with other members of the *C. nigricans* group. They further considered *ferdinandi*, *nigricans*, and *carbonaria* to be each other's closest relatives based on streaked throats in females, a character they called "unusual (presumably derived) among female antbirds." Silva (1992), in his cladistic analysis of the *nigricans* group, also used the narrow white tips to the rectrices to join *manu* and *melanaria*, distinguishing this condition from the broad white tail tips that characterize the other members of the *nigricans* group, as well as *cinerascens*. However, he treated the character of streaked throats in females differently

TABLE 1
LENGTH (MM) OF WHITE TIPS OF RECTRICES FOR VARIOUS TAXA IN THE *CERCOMACRA NIGRICANS* GROUP

Taxon	Mean	(SD; N)
C. cinerascens cinerascens	3.9	(1.04; 6)
C. cinerascens sclateri	7.7	(0.91; 6)
C. cinerascens immaculata	3.0	(0.73; 10)
C. melanaria	2.8	(1.31; 3)
C. manu	4.7	(1.30; 9)
C. carbonaria	7.2	(0.76; 5)
C. nigricans	7.8	(1.16; 12)

from Fitzpatrick and Willard. Silva considered *carbonaria* to have an unstreaked throat, and *manu* and *melanaria* to have "slightly marked" throats in contrast to the "well marked" throats of *ferdinandi* and *nigricans*.

Based on our examination of specimens at FMNH and LACM, we believe that Silva's analyses of both the white tail tips and the underpart pattern (including throat streaking) of females need modification. Although Silva (1992) treated *C. cinerascens* as having broad white tips to the rectrices, the width of the white tips in *C. cinerascens* shows substantial geographic variation (Table 1). The subspecies *sclateri* has white tips fully as wide as *C. carbonaria*, a species treated by Silva as having broad tips, but *C. c. immaculata* and nominate *cinerascens* have white tips that are narrower than in *C. manu*, one of his species with narrow white tail tips. As a result of this variation within a species, it seems inappropriate to use the width of the white tail tips as a character in a phylogenetic analysis within this group of *Cercomacra*.

Similarly, although Silva treated *cinerascens* as lacking throat streaks in contrast to the "slightly marked" throats of *manu* and *melanaria*, we find that the pattern of *cinerascens* is quite similar to that of *manu*. Four female specimens of *manu* have medium-gray underparts with the rachis of some feathers of the throat and upper breast white, forming a subtle, narrow streaking. In *cinerascens*, females (15 specimens) typically show a pale rachis, contrasting with darker barbs, on feathers of the throat and upper breast, but because the pale rachis is buff and the remainder of the feather is ochraceous, the contrast appears less strong than in *C. manu*, even though the pattern is the same in the two species. Silva's treatment of *carbonaria* females as having unstreaked throats appears questionable as well. The female of that species has much whiter underparts than any other *Cercomacra*, and these underparts are variably streaked, spotted,

and blotched with black, gray, and buff. The throat of one FMNH female specimen is largely whitish, marked irregularly with black and gray, and three others (LACM) have white throats moderately to heavily streaked with black and gray. Feathers on the upper breast closely resemble the white streaked feathers of females of *C. nigricans* with broad white centers edged with dark gray or black. This agrees with our field observations, none of which indicate that female *carbonaria* have anything other than streaked throats. Because of this, we propose that females of *C. carbonaria* are best treated as showing the streaked pattern of *nigricans* and *ferdinandi*, as was done by Fitzpatrick and Willard (1990).

In addition, interpretation of relationships within the *Cercomacra nigricans* group have been hampered by lack of recorded, comprehensive vocal repertoires for each species (Fitzpatrick and Willard 1990, Silva 1992). None of these workers had access to tape recordings of *C. carbonaria*, and only Silva (of the three) had field experience with the bird. Furthermore, in 1990 there were almost no known recordings of *C. ferdinandi* available for study, and the voices of the just-described *C. manu* and the range-restricted *C. melanaria* were only marginally better represented in sound collections.

Both Fitzpatrick and Willard (1990) and Silva (1992) identified the characteristic two-syllable element in the primary song as a phylogenetically informative character. It unites the *nigricans* group in Fitzpatrick and Willard (1990), and Silva (1992) used it as a character to identify the clade including the *nigricans* group and *cinerascens*. Fitzpatrick and Willard (1990), in their analysis, reported a "staccato whinny" vocalization for *C. manu*, and noted that "only *manu*, *melanaria*, and *ferdinandi* are known to have the staccato whinny in their repertoire." Based on these statements, Silva (1992) used the presence or absence of the "staccato whinny" as a character in constructing his cladograms for the *C. nigricans* group. He scored the character as being absent in *C. carbonaria* (based on his own field experience) and present in *manu*, *melanaria*, and *ferdinandi* (based apparently on the statements of Fitzpatrick and Willard). The resulting cladogram was discordant with the hypotheses of Fitpatrick and Willard with respect to the phylogenetic position of *C. ferdinandi*, which Silva (1992) considered as the sister species of the *manu-melanaria* clade.

While acknowledging that verbal transcriptions of bird vocalizations often lose something in the translation from one observer to the next, we remain unclear as to which of *C. manu*'s many vocalizations is the "staccato whinny." The vocalization that sounds closest to Fitzpatrick and Willard's (1990) description (Fig. 3A) does appear to have analogous elements in the repertoires of *C. melanaria* (Fig. 3B) and *C. ferdinandi*

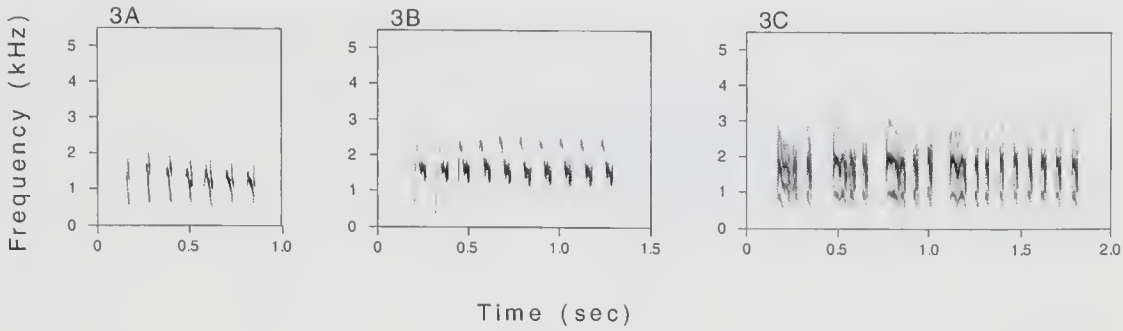
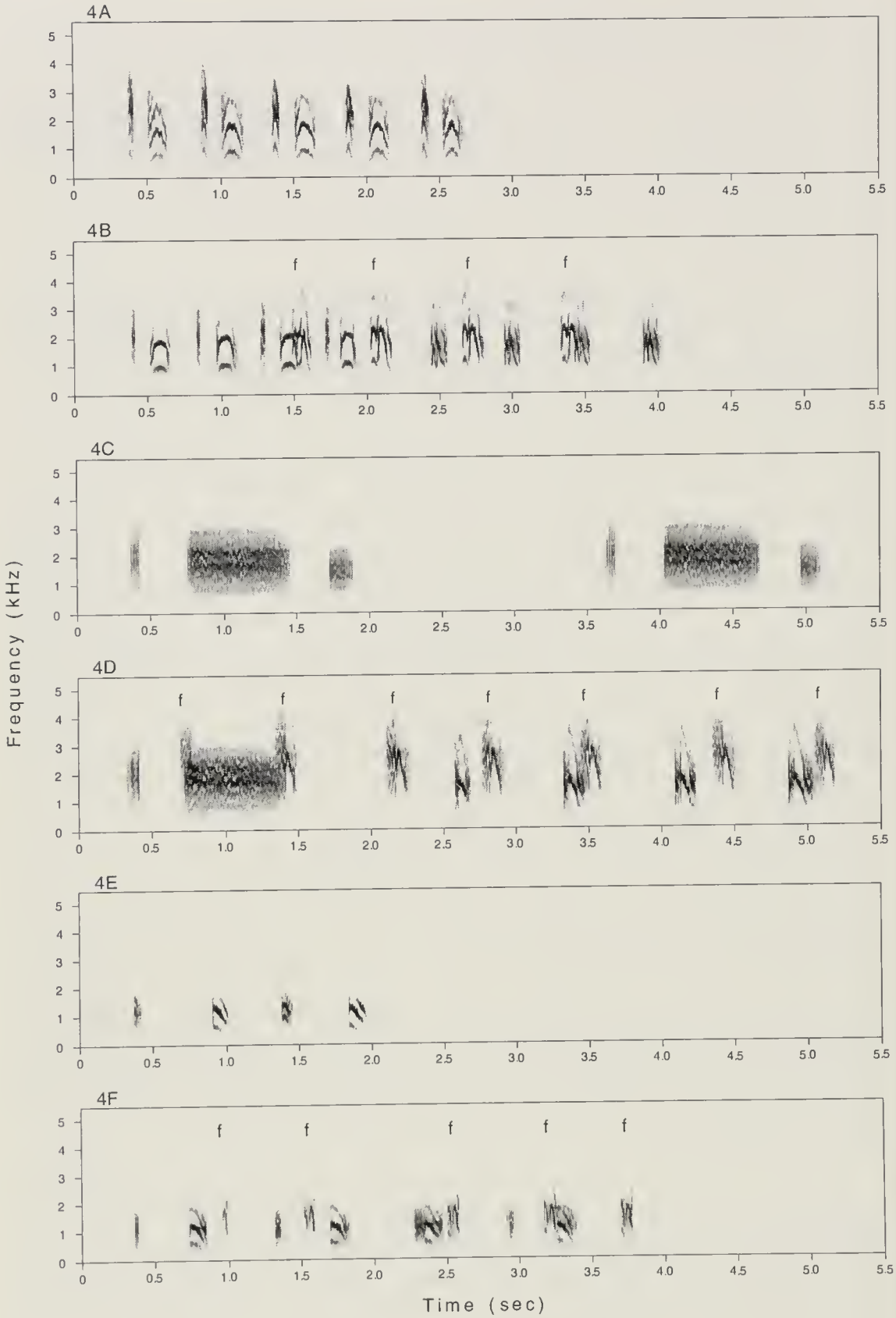


FIG. 3. Sonagrams of "staccato whinny" vocalizations of *Cercomacra* antbirds: (A) "whinny" of Manu Antbird (*C. manu*) from Madre de Dios, Peru (K. J. Zimmer recording), (B) "whinny" of Mato Grosso Antbird (*C. melanaria*) from Mato Grosso, Brazil (R. Behrstock recording), and (C) song with "whinny" element of Bananal Antbird (*C. ferdinandi*) from Goias, Brazil (P. Donahue recording).

(Fig. 3C). However, the "whinny" elements of each of the three species appear only tenuously related. The "whinny" of *manu* is a frequently heard vocalization (but given at irregular intervals) that may be repeated several times in succession, independent of other vocalizations (Zimmer, pers. obs.). It is often given by foraging birds visually separated from their mates and is more commonly heard in mid-day or afternoon (Zimmer, pers. obs.). The "whinny" element of *ferdinandi* does not appear to stand alone as a distinct vocalization, but rather, is joined to the end of the two-note element to produce a more complex primary song (Isler and Whitney 1996, Fig. 3C). We do not know the context of the "whinny" vocalization in *melanaria*. In our collective field experience with *melanaria*, we have not noted any similar vocalization, and we could only locate a single archived recording of this call (Fig. 3B). Whatever the function, the "whinny" does not seem to be a commonly used part of the vocal repertoire of *C. melanaria*. Our work with *C. carbonaria* certainly supports Silva's (1992) contention that no such vocalization is included in the vocal repertoire of that species; however, it could be present but rarely used (as in *C. melanaria*). We would argue that too much weight has been given to the presence or absence of the "staccato whinny," given that the vocalization seems to differ widely in both function and frequency of use between taxa.

At the same time, some vocal similarities between *C. carbonaria* and other species in the group have been overlooked. The primary, "hitch-COCK" song and the male-female duets of *C. carbonaria* sound closest to recordings of the analagous vocalizations of *C. nigricans* (Fig. 4A, 4B), observations that fit well with the hypotheses of both Silva (1992) and Fitzpatrick and Willard (1990). However, there are also some vocal similarities between *C. carbonaria* and *C. melanaria* that could suggest


4A
4B
4C
4D
4E
4F
f
Frequency (kHz)
Time (sec)
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
1
2
3
4
5

a closer relationship between those taxa than previously suggested. The primary song of male *C. melanaria* is a three-note "rek-RURRRR-rock," with the middle note much longer than the other two (Fig. 4C). Females sing a nearly identical song that differs slightly in pitch. Although these songs are quite different from the primary song given by males of *C. carbonaria*, qualitative similarities in tone and note shape are evident between the middle note of the *melanaria* song and the "squeaking branch" calls (Fig. 2D) given by both sexes of *carbonaria*. More striking are the similarities in the duets of the two species. Duets of *C. melanaria* typically begin with one or more male songs, after which the female begins interjecting a loud, sharp "ECK" note (Fig. 4D) similar to that of female *carbonaria*. This "ECK" note may be inserted anywhere in the middle of the male's song or immediately after the third note of the song. As in *C. carbonaria*, a few notes by the female *C. melanaria* typically results in the male switching from its song to a single loud "OWP," which is less squeaky and slightly lower-pitched than the female's "ECK" (Fig. 4D). Both birds then proceed to deliver an antiphonal duet of alternated "ECK" and "OWP" notes at the rate of about 3–4 combined notes per second for 4–8 seconds. Occasionally the roles will be reversed, with females singing the primary song and the male initiating the duet of single notes. As can be seen from comparing sonagrams in Figures 2 and 4, the duets of *C. carbonaria*, *C. nigricans*, and *C. melanaria* are similar in overall pattern and cadence, and in the shape and pitch of the individual notes of both the males and the females. As is the case with *C. carbonaria*, duets of *C. melanaria* usually end with the male delivering the terminal note.

In our experience, *Cercomacra manu* has the most extensive vocal repertoire of any species in the *nigricans* group. We have recorded several vocalizations of *C. manu* for which there seems to be no analogs in the repertoires of the other species. The primary song given by males is a two-noted "uck OCK," with the individual notes spaced about 0.5 sec apart (Fig. 4E). These notes may be repeated monotonously, or the ca-

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FIG. 4. Sonagrams of vocalizations of *Cercomacra* antbirds: (A) songs of male Jet Antbird (*C. nigricans*) from Darién, Panama (T. A. Parker recording, LNS #25923), (B) Jet Antbird: male songs leading into male–female duets, from Miranda, Venezuela (P. Schwartz recording), (C) songs of male Mato Grosso Antbird (*C. melanaria*) from Mato Grosso, Brazil, (D) Mato Grosso Antbird: male song leading into male-female duet, from Mato Grosso, Brazil, (E) songs of male Manu Antbird (*C. manu*) from Mato Grosso, Brazil, and (F) Manu Antbird: male song leading into male-female duet, from Mato Grosso, Brazil. Unless otherwise noted, sonagrams are from recordings by K. J. Zimmer.

dence may be varied, as in "uck OCK OCK, uck OCK." Males also routinely sing a faster series of 3-6 "uh-oh" couplets, at a lower pitch. Although these songs are recognizably similar to those of other species in the *nigricans* group, they also differ markedly in frequency and pace (Fig. 4E). Duets often consist of females inserting loud, single "OUK" or "CLOCK" notes into typical male songs, the notes being placed either immediately after the second male note, in between the notes, or superimposed over one of the male notes (Fig. 4F). This usually stimulates the male to switch from the two-note song to a cadenced series of single notes, as is the norm for other species in the *nigricans* group. At this point however, females often switch from single notes to a series of 2–5 "uh-ouk" couplets, the notes of which are more nasal in quality and much more closely spaced than the two-noted songs of males (Fig. 4F). Contrary to the pattern seen in duets of *C. carbonaria*, *C. nigricans*, and *C. melanaria*, duets of *C. manu* routinely end with the female delivering the terminal note or notes.

In overall duet pattern, frequency band of individual notes, and stereotyped behavior of males in delivering terminal notes, the duets of *carbonaria*, *nigricans*, and *melanaria* are all more similar to one another than any of them is to *manu*. Unfortunately, the scarcity of tape recordings of *C. ferdinandi* precludes any assessment of duets or vocal repertoires of that species, making hypothesized relationships tenuous.

A cladistic analysis of relationships within the *C. cinersascens* complex may be premature, even with the addition of the vocal characters discussed above. However, we will discuss some preliminary thoughts on relationships within the group. The complex can be recognized as a clade within *Cercomacra* as described by Silva (1992). Two characters, white tail-tips, and a distinctive form of the primary vocalization, support this clade. Furthermore, Silva's placement of *cinerascens* as a sister species to the remainder of the group appears sound. The other species can be joined as a clade based on females with grayish, rather than brownish underparts, and with male plumage largely blackish. Beyond this, the only informative character that has been detected in the plumage analysis thus far is the heavy streaking on the throats of females of *nigricans*, *carbonaria*, and *ferdinandi*. This unites these species in a group that cannot be further resolved at present. This clade, *manu*, and *melanaria* form a trichotomy that cannot be resolved with plumage characters. The close similarity between *manu* and *melanaria* in female plumages is due to sharing primitive features within the group, rather than evidence of a sister relationship as hypothesized by Fitzpatrick and Willard (1990). The vocal characters discussed above, especially similarities between *melanaria* and *carbonaria*, and in the duet pattern of those species and *nigricans*, suggest

that *melanaria* is more closely related to the *nigricans*, *carbonaria*, *ferdinandi* group than to *manu*. The lack of information for *ferdinandi* as well as limited material for some other members of the genus (especially of duets) makes this a tentative suggestion. Biochemical data and further analysis of vocal data will be necessary to completely understand relationships within the *Cercomacra nigricans* group. Particular attention should be paid to male-female antiphonal duets, which are a conspicuous feature of the genus *Cercomacra*, and which may prove important indicators of relationship.

The gallery forests which *Cercomacra carbonaria* inhabits are part of a complex of open habitats, locally called "lavrado", dominated by dry grasslands in northeastern Roraima (Vanzolini and Carvalho 1991). Besides *C. carbonaria*, the region holds another endemic bird, Hoary-throated Spinetail (*Poecilurus kollari*), and the only Brazilian populations of several other species of birds. Other groups of organisms also have endemic taxa restricted to this region (Vanzolini and Carvalho 1991). These open habitats are almost completely unprotected, the exception being small patches of grassland totaling less that 1000 ha at the Maracá Ecological Station. Neither endemic bird occurs at Maracá.

Cercomacra carbonaria is treated by Collar et al. (1992) as "vulnerable", indicating "taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating." The small range of *Cercomacra carbonaria* contributes to its vulnerable status, as does the complete absence of habitat protection. The most critical problem facing this species is the restricted area of gallery forest in the region and the potential threats to that habitat. Although there do not appear to be serious immediate threats to the gallery forests, they appear to be most at risk among the habitats within the lavrado of Roraima. There has been some conversion to agriculture, especially rice cultivation, and some trees in the gallery forest are used for their wood. In addition, however, our studies suggest that attention should focus on river islands with extensive gallery forest, where *Cercomacra carbonaria* is much more common than in mainland gallery forest sites, as described above. We urge protection for at least Ilha Boa Agua and Ilha São Jose, where *Cercomacra carbonaria* is most abundant, together with areas of gallery forest on the adjacent mainland. This would protect a major population of *C. carbonaria*, as well as other species restricted to the gallery forest of this region.

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MIGRATION BEHAVIOR OF TUNDRA SWANS FROM THE YUKON-KUSKOKWIM DELTA, ALASKA

CRAIG R. ELY,[1,3] DAVID C. DOUGLAS,[1] ADA C. FOWLER,[1]
CHRISTOPHER A. BABCOCK,[1] DIRK V. DERKSEN,[1] AND J. Y. TAKEKAWA[2]

ABSTRACT.—Tundra Swans (*Cygnus columbianus columbianus*) fitted with satellite transmitters (PTTs) on the outer coast of the Yukon-Kuskokwim (Y-K) Delta, Alaska, migrated eastward across the Y-K Delta in late September and stopped at wetlands on the west side of the Alaska Range during early October. After crossing the Alaska Range, swans stopped briefly on the Susitna Flats of Upper Cook Inlet. They then migrated eastward into the Yukon, Canada, and from there flew southward, paralleling the Wrangell Mountains through the interior of the Yukon to a staging area in northeastern British Columbia. They gradually migrated through central Alberta and southwest Saskatchewan and across Montana to a staging area in southeastern Idaho. They remained in southeastern Idaho from mid-November until early December when they migrated across Nevada to the Sacramento-San Joaquin Delta of California. Spring migration routes were similar to those used in autumn. Band returns and observations of neck-banded swans corroborated the general autumn and spring migration routes of PTT-marked birds. Swans stopped only briefly (<3 days) at staging areas in Alaska and northern Canada but lingered at migration areas in Alberta, Saskatchewan, and Idaho. *Received 23 Oct. 1996, accepted 15 April 1997.*

Despite their conspicuousness, we have a poor understanding of Tundra Swan (*Cygnus columbianus columbianus*) migration pathways. Information is particularly lacking from northern migration areas, especially for Tundra Swans originating from the Yukon-Kuskokwim (Y-K) Delta, the most important breeding area for the species in North America (Sladen 1973, Sladen and Kistchinski 1977, Bellrose 1980).

Swans from the Y-K Delta are part of the western population that nests in Alaska on coastal tundra habitat from Kotzebue Sound, south to Bristol Bay and Kodiak Island, and westward to Unimak Island on the Alaska Peninsula (Wilk 1988, Limpert et al. 1991, Spindler and Hall 1991). Swans from the western population winter in 12 Pacific Flyway states and the province of British Columbia, with most wintering in California (Sherwood 1960, Bellrose 1980, Paullin and Kridler 1988). It is unknown if swans from specific breeding areas within the western population have affinities for discrete wintering and staging areas.

Here we present results from a study that tracked the movements of

[1] Alaska Science Center, Biological Resources Division, U. S. Geological Survey, 1011 E. Tudor Road, Anchorage, Alaska 99503.
[2] California Science Center, Biological Resources Division, U. S. Geological Survey, P. O. Box 2012, Vallejo, California 94592.
[3] Corresponding author.

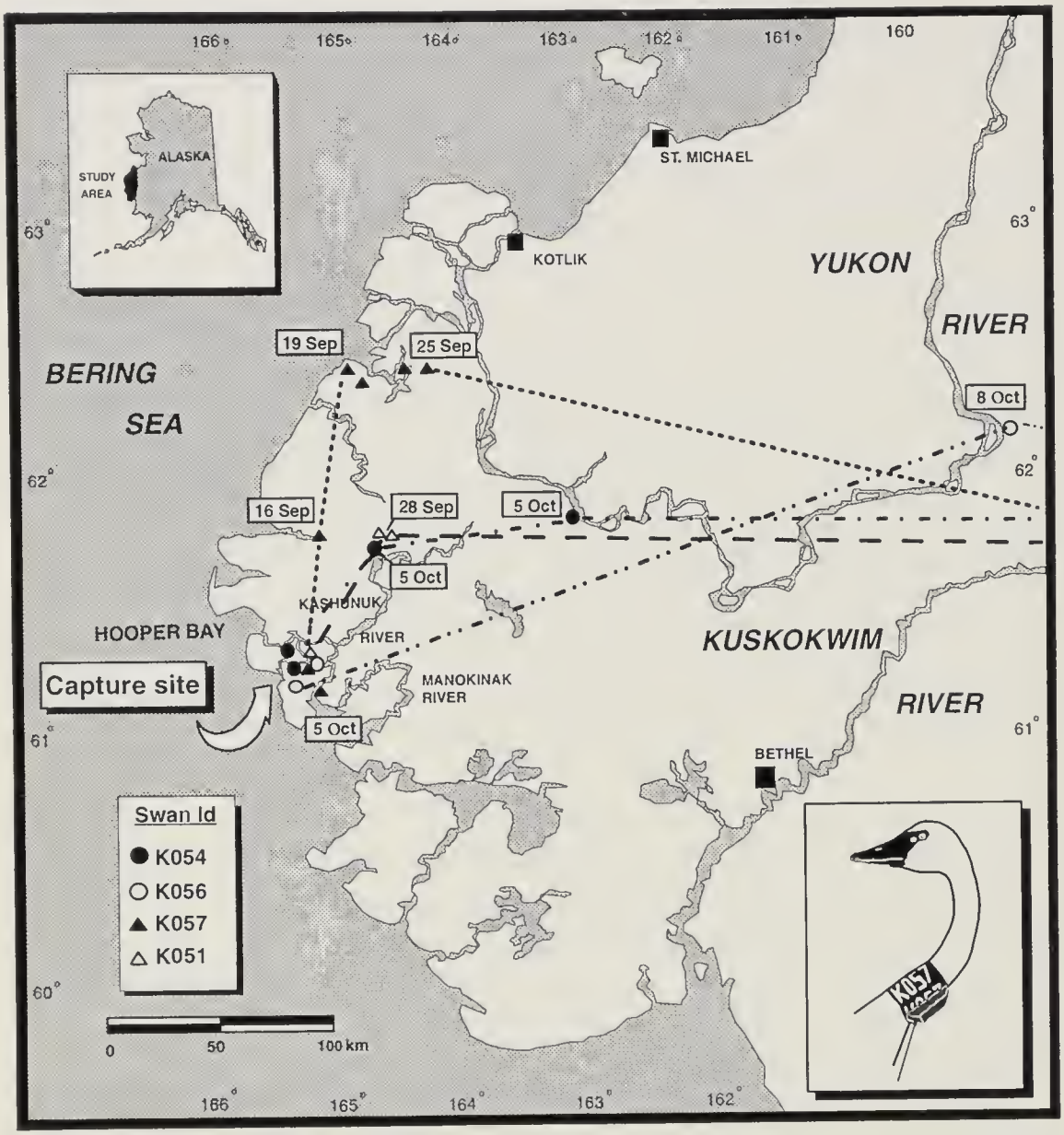

FIG. 1. Movements of four PTT-marked Tundra Swans during September and early October on the Yukon-Kuskokwim Delta, Alaska, in 1994. Inset—Tundra swan with satellite transmitter glued onto plastic neck band.

satellite-marked Tundra Swans during autumn and spring migration between the outer Y-K Delta and wintering areas in California. We compare our results with the distribution of observations of swans we neck-banded and with the recoveries of birds leg-banded on the Y-K Delta.

STUDY AREA AND METHODS

Seven females with cygnets and two males were captured and fitted with satellite transmitters (platform transmitting terminals, or PTTs) during August 1994 near Old Chevak (61°26′N, 165°27′W) on the outer Y-K Delta, Alaska (Fig. 1). We also captured flightless

swans opportunistically during July and August 1987–1994 and fitted them with plastic coded neck bands (Sherwood 1966, Sladen 1973) and metal U. S. Fish and Wildlife Service leg bands. We used three types of PTTs, built by different manufacturers. The PTTs weighed 30–50 g, and were attached to the neck bands (Higuchi et al. 1991) using epoxy glue (Fig. 1—inset). PTTs were programmed to transmit every 90 s for 4–5 h and then stop transmitting for 43–44 h, thus allocating battery capacity over a longer period of tracking. Expected transmitter life was six months. PTT transmissions were collected by Service Argos (Landover, Maryland) receivers on board two National Oceanographic and Atmospheric Administration (NOAA) polar-orbiting environmental satellites (Fancy et al. 1988, Harris et al. 1990). For each satellite overflight that received two or more transmissions from a PTT, Service Argos calculated its location using the perceived Doppler shifts of the PTTs signal frequency together with satellite position data. The Doppler method of locational derivation resulted in two solutions that Service Argos reports as 'primary' and 'alternate'.

We subscribed to two data processing products offered by Service Argos: Standard Processing and Auxiliary Location Processing (formerly called 'Animal Tracking Service'). Standard Processing provided primary locations for PTTs when four or more signals were received during a satellite overflight and several data processing criteria were met (Argos 1996). Auxiliary Location Processing provided alternate locations for all Standard Processing locations, as well as primary and alternate locations for data that failed Standard Processing criteria, including satellite overflights that only recovered two or three PTT transmissions. Service Argos reported the accuracy of Standard Processing locations to be generally within 1 km, and that use of locational data from Auxiliary Location Processing was at the discretion of the investigator (Petersen et al. 1995).

We used a series of quantitative and qualitative criteria to remove aberrant locations that were typical of animal tracking databases which used the Argos 'Doppler' system (Fancy et al. 1988). We selected one location from each primary/alternate pair (or removed both locations from the database) by considering three factors; minimum travel distance from the previous location, rate of movement from the previous location, and/or locational redundancy with the previous or a subsequent location. Our approach was conservative in that we removed all locations lacking reasonable biological plausibility unless they were validated by subsequent locations in the vicinity.

We summarized distribution information from sightings of neck-banded birds obtained before May 1996 by volunteer observers that were reported either directly to us, to the U. S. Geological Survey Bird Banding Laboratory (BBL), or to state and federal biologists. Multiple observations of the same marked individual were included only if they differed by location, year, or season. We also summarized recoveries of swans leg-banded on the Y-K Delta and reported to the BBL before September 1995.

RESULTS

We obtained sufficient data to interpret the migratory patterns of four of the PTT-marked birds, all of which were adult females. We were unable to document the causes of PTT failure. Likely possibilities included: failure of batteries or electronic components, mechanical breakage of antenna or collar, or swan mortality. Mortality was ruled out for one swan whose PTT failed shortly after deployment but was observed in the Willamette Valley, Oregon, in November–December. Although PTTs were programmed to transmit location information every two days, none of the transmitters provided such information on a consistent basis.

Swans moved only short distances immediately after capture, as expected for adults with cygnets. PTT-marked swans remained near capture sites throughout August and most of September (Fig. 1). After the onset of migration in late September, some transmittered swans stopped along the Bering Sea coast or major rivers before continuing eastward across the Y-K Delta (Fig. 1).

After departing the Y-K Delta, swans used wetlands on the upper Kuskokwim River before crossing the Alaska Range and stopping on the Susitna Flats of Upper Cook Inlet (Fig. 2, site B; Table 1). They then migrated eastward across Alaska into the Yukon Territory and then southward, paralleling the Wrangell Mountains through the interior of the Yukon into northeastern British Columbia. Despite relatively mild autumn weather, swans stopped only briefly (<7 days) at staging areas in Alaska and Yukon Territory (Table 1). From northeastern British Columbia, swans migrated to central Alberta and southwest Saskatchewan where they remained for up to three weeks during late October and early November before flying across Montana to southeastern Idaho. They remained near the Snake River in southeastern Idaho from mid-November until early December when they migrated across Nevada to the Sacramento-San Joaquin Delta of California.

Two PTTs functioned longer than expected and provided location information throughout winter and during spring migration (Tables 1, 2). One swan (K056) wintered in both the Sacramento-San Joaquin Delta and the Sacramento Valley, moving between the two areas several times during December-February. The other swan (K054) remained in the Sacramento-San Joaquin Delta. The swans took different spring migration routes: K056 migrated north through Oregon and Idaho to Alberta, while K054 flew east to Utah before continuing north into Montana (Fig. 3, Table 2). Although the two swans used different routes, the timing of migration was similar. Both departed California in late February and arrived in Idaho and Montana the third week of March.

Our estimates of the maximum rate-of-movement ranged from 60–90 kph (N = 12). To reduce the influence of location error on estimates of distance travelled between locations, we restricted our analysis of rate-of-movement to instances when ≥30 min expired between consecutive locations and/or the distance travelled was ≥50 km. The majority (N = 9) of our maximum estimates were obtained from three birds migrating during 13–18 October from eastern Alaska to British Columbia and Alberta, where satellite coverage was still optimum (Fancy et al. 1988).

The general route of migrating swans (Figs. 2, 3) was corroborated by

TABLE 1

AUTUMN MIGRATION AND WINTERING AREAS USED BY TUNDRA SWANS MARKED WITH SATELLITE TRANSMITTERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA IN 1994

Map reference[a]	State/Province	Geographic location	Coordinates		Swan Id.	Location		No. locs[b]
			Lat.	Long.		First	Last	
A	Alaska	W. side of Alaska Range	61.347	154.615	K054	7 Oct	7 Oct	1
		Stony River	61.606	154.657	K056	9 Oct	9 Oct	1
		S. Kuskokwim	62.649	153.860	K051	10 Oct	10 Oct	1
B	Alaska	Cook Inlet	61.287	150.255	K054	10 Oct	10 Oct	1
			61.235	150.266	K056	12 Oct	13 Oct	2
C	Alaska	Tetlin	62.614	142.077	K056	14 Oct	15 Oct	1
D	Yukon	NE Kluane	61.812	137.378	K051	12 Oct	12 Oct	1
E	Yukon	Watson Lk.	60.454	125.411	K054	13 Oct	14 Oct	4
F	British	Ft. Nelson/	58.201	122.778	K051	16 Oct[b]	16 Oct	1
	Columbia	Liard River	59.186	123.919	K054	14 Oct	18 Oct	4
G	Alberta	Battle River Area	52.676	112.150	K054	22 Oct	24 Oct	4
		(150 km SE Edmonton)	52.375	111.608	K056	22 Oct	28 Oct	7
			52.446	110.804	K057	10 Oct	16 Oct	6
H	Saskatchewan	Southwest	49.253	109.233	K057	22 Oct	2 Nov	6
			49.847	109.175	K054	30 Oct	30 Oct	1
I	Idaho	Snake River	43.066	112.704	K054	12 Nov	5 Dec	10
		(Southeast)	43.167	112.924	K056	15 Nov	4 Dec	7
J	Nevada	Ruby Lake Northeast	40.309	115.906	K057	10 Nov[c]	10 Nov	1
			41.448	117.080	K054	11 Dec	11 Dec	1
K	California	Sacramento–San Joaquin	38.152	121.547	K054	22 Dec	9 Feb	51
		Delta	38.417	121.653	K056	6 Jan[d]	9 Feb	12
L	California	Sacramento Valley	39.401	121.755	K056	27 Dec	17 Feb	5

[a] See Fig. 2.
[b] Number of locations in the vicinity; usually only one "fix" at the exact coordinates. Locations based on only one set of coordinates may have been birds in flight.
[c] Last location information for this PTT.
[d] K056 moved several times between areas K and L from late December through mid-February.

TABLE 2

SPRING MIGRATION AREAS USED BY TUNDRA SWANS MARKED WITH SATELLITE TRANSMITTERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA IN 1994

Map reference[a]	State/ Province	Geographic location	Coordinates		Swan Id.	Location		No. locs[b]
			Lat.	Long.		First	Last	
M	Oregon	Klamath Marsh	42.903	121.644	K056	28 Feb	18 Mar	5
m	Utah	Salt Lake	41.534	112.094	K054	27 Feb	3 Mar	2
n	Montana	Freezeout Lake	47.665	112.141	K054	19 Mar	19 Mar	1
N	Idaho	Coeur d'Alene	47.305	116.506	K056	20 Mar	24 Mar	2
o	Alberta	Milk River	49.121	110.474	K054	14 Apr	20 Apr	3
O	Alberta	Vauxhall–SE Calgary	50.147	112.329	K056	2 Apr	2 Apr	1
p	Montana	Cut Bank	48.718	112.157	K054	22 Apr	10 May[c]	2
P	Alberta	Red Deer River[d]	51.876	113.052	K056	6 Apr	16 Apr	9
Q	Alberta	Lesser Slave Lk.	55.425	115.430	K056	18 Apr	18 Apr	2
R	Alberta	Peace River	55.885	118.096	K056	22 Apr	26 Apr	3
S	Yukon	Teslin Lake	60.245	132.605	K056	27 Apr	27 Apr	1
T	Alaska	Tetlin	62.908	141.631	K056	29 Apr	29 Apr	5
U	Alaska	Holy Cross	62.114	159.818	K056	1 May[c]	1 May	2

[a] See Fig. 3.
[b] Number of locations in the vicinity; usually only one "fix" at the exact coordinates. Locations based on only one set of coordinates may have been birds in flight.
[c] Last location information for this PTT.
[d] Range of latitude 51.105–51.876 and longitude 112.758–113.530.

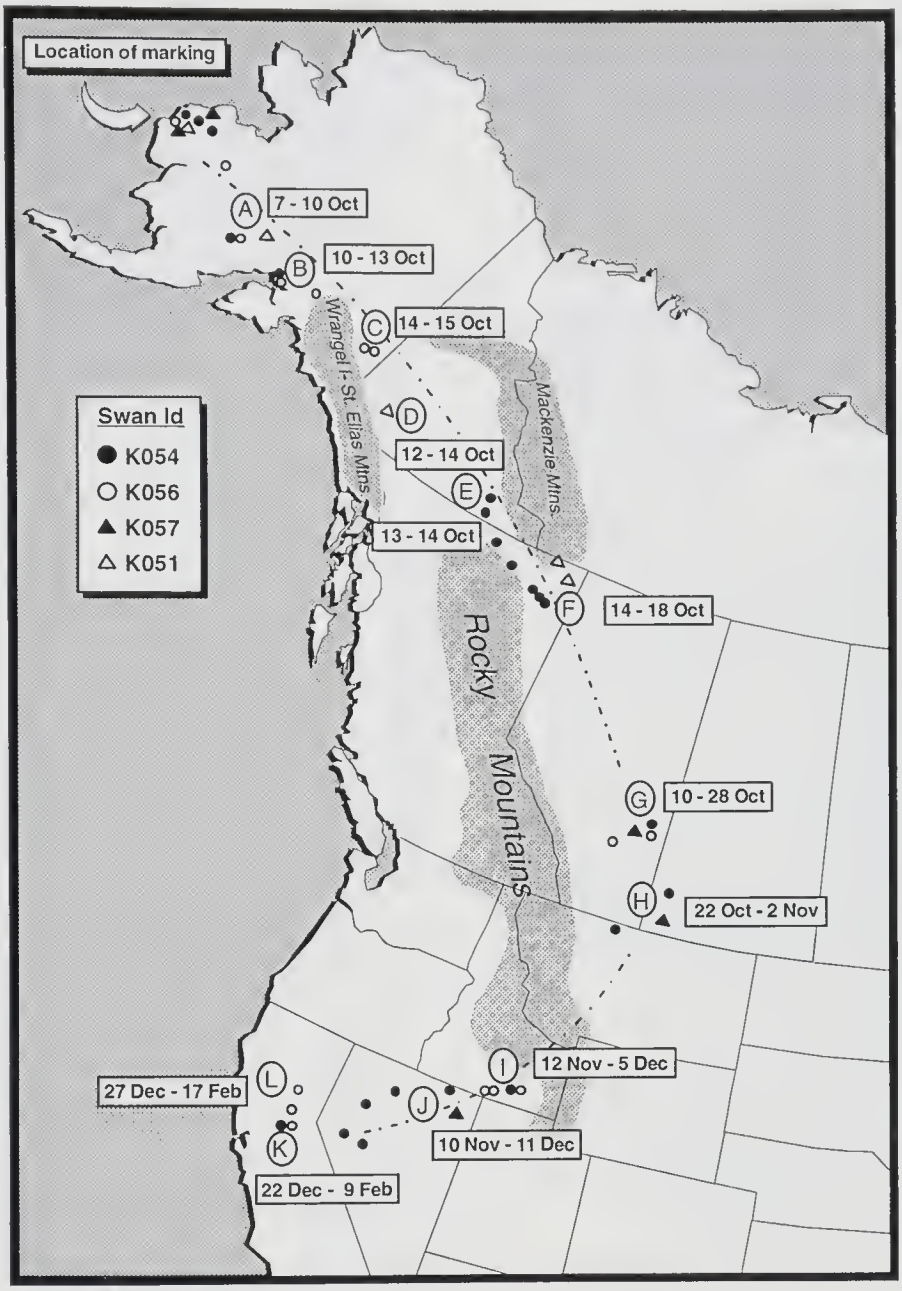

FIG. 2. Autumn migration route of four PTT-marked Tundra Swans from their breeding grounds on the Yukon-Kuskokwim Delta, Alaska to their wintering grounds in California. Letters refer to locations described in Table 1.

regional biologists that noted flocks of swans in many of the geographic areas used by PTT-marked birds. The distribution of recoveries of leg-banded swans and observations of neck-banded swans from the Y-K Delta differed slightly from the distribution of locations of PTT-marked birds (Fig. 4). Seventeen percent (16 of 92) of the observations and recoveries were in northern Utah whereas only one PTT-marked bird visited this

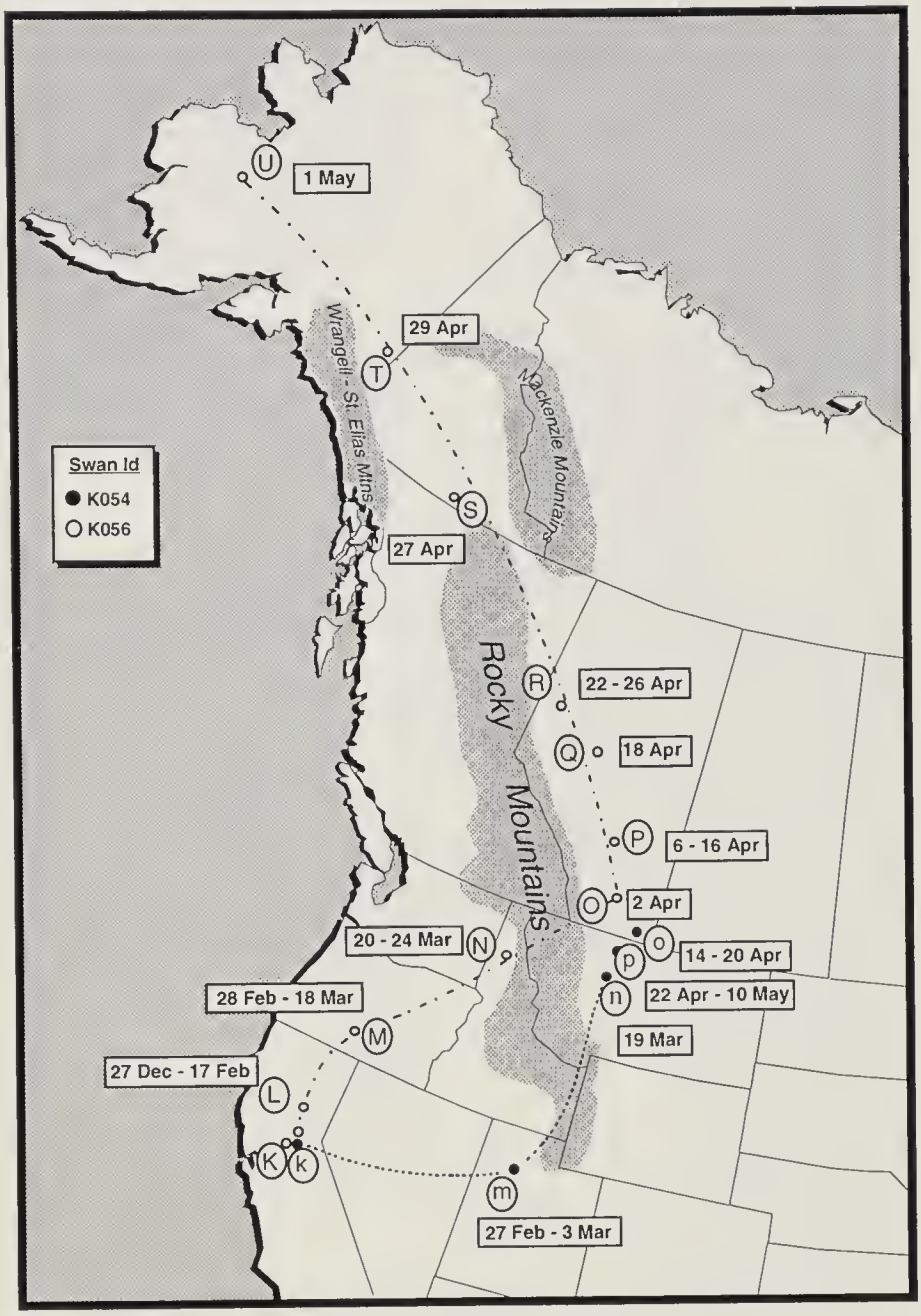

FIG. 3. Spring migration routes of two PTT-marked Tundra Swans from their wintering grounds in California to their breeding ground on the Yukon-Kuskokwim Delta, Alaska. Letters refer to locations described in Table 2.

area. Similarly, nearly 12% (11 of 92) of the recoveries and observations of swans were in Oregon, Washington, or southwestern British Columbia. None of our swans with functioning transmitters visited these areas, although one swan with a failed PTT was observed in November and December in northwestern Oregon. In contrast, the PTT-marked swans used many areas in Canada and Alaska for which there was very little if any observation or recovery data.

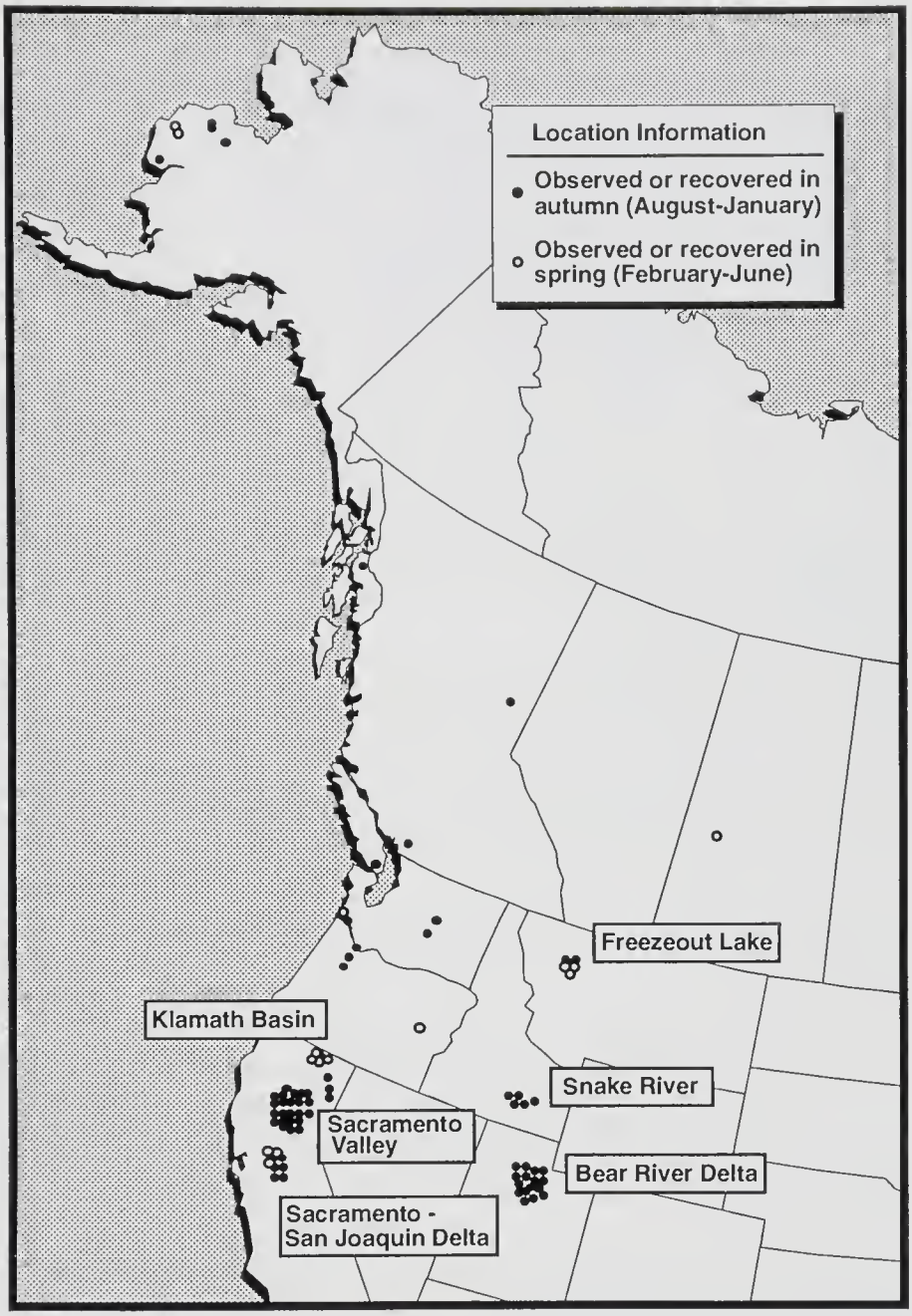

FIG. 4. Distribution of observations and recoveries of leg-banded (N = 46) and neck-banded (N = 46) Tundra Swans from the Yukon-Kuskokwim Delta, Alaska. Does not include one direct recovery in Georgia and one direct recovery in Texas.

Resightings of neck-banded swans at more than one location during the same year provided additional information on migration routes. A neck-banded pair was observed at Freezeout Lake, Montana, in late October and subsequently observed on the Bear River Delta of Utah in early December. Another swan observed in the Sacramento Valley in late January was seen at Freezeout Lake in late February.

DISCUSSION

Tundra Swans on the Y-K Delta generally do not fledge until September, and some not until October (Lensink 1973). Hence, it is not surprising that PTT-marked swans, all of which were with young, generally remained near marking locations through September. Swans likely undertook local movements during late September and early October (Fig. 1) to join other swans prior to autumn migration (Kear 1972).

Several different migration routes have been proposed for the western population of Tundra Swans, based largely on surveys and a few band recoveries. Sladen (1973) and Bellrose (1980) indicate three possible pathways are used: (1) Coastal route from south central Alaska, along British Columbia to Washington; (2) British Columbia route from central Alaska through interior British Columbia to Washington; and (3) Trans-Rocky Mountain route, similar to what we have reported here, but originating in eastern Alaska.

Our PTT-marked swans did not migrate via a coastal route or through interior British Columbia. The only evidence of the use of a coastal route by Y-K Delta swans, is a single recovery of a leg-banded swan in southeast Alaska (Fig. 4). The coastal route is most likely used by Tundra Swans from the Alaska Peninsula and Bristol Bay (Bellrose 1980). Recoveries and observations of swans in Washington and British Columbia (Fig. 4) indicate some Y-K Delta swans migrate via the interior British Columbia route.

PTT-marked swans used a trans-Rocky Mountain route during autumn and spring migrations. This general migratory pathway is thought to be the most commonly used, with some variations concerning specific portions of the route (Sherwood 1960, Bellrose 1980, Pacific Flyway Study Committee 1983, Paullin and Kridler 1988). Our data showed no use of Lake Athabasca in northeastern Alberta, considered by Bellrose (1980) to be an important autumn staging area for Tundra Swans from western Alaska. It may be that western population swans do not stop there (e.g., Sladen 1973, but see Limpert et al. 1991), that it is used by western swans from other nesting areas, or that we had too few PTT-marked birds to determine the importance of the area to Y-K Delta swans. Bellrose (1980) thought interior-migrating swans followed two corridors after arriving in Alberta; one equivalent to the route taken by our PTT-marked swans through western Montana, and the other a path across northern Idaho to eastern Oregon and south to the Klamath Basin of California.

Paullin and Kridler (1988) also reported autumn movements of swans from eastern Oregon to the Klamath Basin, and to the Willamette Valley of western Oregon. The latter pathway may have been the route taken by

one of our swans with a non-functioning PTT observed in the Willamette Valley, Oregon in early November (M. Naughton, pers. comm.).

During spring, the two different trans-Rocky Mountain routes used by the PTT-marked swans (Fig. 3) were similar to pathways reported for dye-marked swans of unknown breeding origin marked in eastern Oregon (Paullin and Kridler 1988). Northern Idaho and Utah are well known as important spring staging areas for Tundra Swans (Bellrose 1980).

Relocations of our PTT-marked and neck-banded swans showed no indication of birds using migration or staging areas of the eastern population (all Tundra Swans breeding north and east of Kotzebue Sound, and wintering along the Atlantic Coast—Limpert et al. 1991). However, two of 92 (2%) swans leg-banded on the Y-K Delta were recovered from migration and wintering areas of the eastern population. Strong fidelity to migration and wintering areas was also reported by Limpert et al. (1991), who found only one of 25 (4%) Tundra Swans neck-banded on the Y-K Delta outside the normal migration and wintering areas of the Western Population. Mixing of swans from the eastern and western populations is thought to occur at staging areas near Lake Athabasca, Alberta (Bellrose 1980, Limpert et al. 1991), the MacKenzie Delta (Paullin and Kridler 1988) and also at Freezeout Lake, Montana (M. Schwitters, pers. comm.).

Tundra swans cygnets are among the slowest of northern waterfowl to grow (Bellrose 1980), and they fledge at a smaller proportion of adult mass than geese (Sedinger 1992). Tundra Swans on the Y-K Delta become volant nearly three weeks after sympatric nesting Cackling Canada Geese (*Branta canadensis minima*) and Greater White-fronted Geese (*Anser albifrons frontalis*), but all three species generally begin autumn migration in late September or early October (Lensink 1973; C. Ely, unpubl. data). Cygnets are thus developmentally less mature than goslings at the beginning of migration and are likely less able to sustain long, uninterrupted flights. It was thus not unexpected that swans made many stops to rest and replenish body reserves during autumn migration. We were surprised however, that swans remained so briefly at northern areas, and did not stop to stage for more than a few days, until they reached central Alberta. Swans have generally been reported to be able to remain longer than geese at northern breeding and staging areas due to the thermoregulatory benefits of large body size and the greater availability of aquatic compared to terrestrial foods after autumn snowfall. However, newly fledged cygnets are much smaller than adult swans, and young accompanied by their parents are often the first to arrive on wintering areas (Kear 1972).

We were only able to monitor PTT-marked swans for one year, but there is evidence of annual variation in timing and use of migration areas.

One PTT-marked swan (K056) that was in southeastern Idaho from 15 November through 4 December 1994 and then on the Sacramento-San Joaquin Delta on 27 December 1994 (Table 1), was observed in the Klamath Basin of northeastern California on 30 November 1995. It is evident that K056 completed migration earlier in 1995 than 1994. K056 may also have altered its migration route between years. Alternatively, K056 may have migrated through the Klamath Basin in early December 1994 before arriving in the Sacramento-San Joaquin Delta.

Our estimate of a maximum speed of migration of 60–90 kph was less than the maximum flight speed of 135 kph speed reported for a Tundra Swan tracked during spring migration with conventional (VHF) telemetry (Alerstam 1990:242). It was, however, similar to the 73 kph ground speed reported by Sladen and Cochran (1969) for a VHF radio-marked juvenile Tundra Swan tracked during spring migration. Flight speeds of swans are highly variable due in part to the presence of head and tail winds associated with weather systems (Ogilvie 1972). Also, flight speeds might be greater in spring (e.g., Alerstam 1990) when adults are not accompanied by young.

Tundra Swans are one of the largest species of flying birds, and one of the first species of birds to be fitted with satellite transmitters. Satellite transmitters have been successfully used to track Bewick's Swans (*Cygnus c. bewickii*) during spring migration in Europe (Nowak 1990) and Asia (Higuchi et al. 1991), where the main objective was to locate the breeding areas of birds marked during winter. Satellite transmitters used on birds are generally smaller and have less battery capacity and are configured to transmit with less signal strength compared to PTTs typically used on large terrestrial mammals (see Caccamise and Hedin [1985] for review of avian transmitter loads). As a result, location information obtained from small avian PTTs is often only accurate to within a few kilometers (Ely et al. 1993, Petersen et al. 1995). Fortunately for studies of species undergoing long migrations, the magnitude of location error is generally negligible relative to the length of the migration route.

Spurious results are always possible when relying on small samples of experimental birds to determine behavior patterns. There is also a degree of subjectivity involved in choosing the "best" set of possible coordinants from the Argos processing system (Fancy et al. 1988). When possible, we tried to verify the use of specific staging areas with visual observations. Verification of southern staging areas was also provided by observations of neck-banded swans and recovery information from leg-banded birds.

Neck band observations and band recovery information (Fig. 4) complemented the PTT data. Banding data provided distribution information

on many nearly non-experimental (leg band only) swans over a period of years, but was somewhat misleading because of both temporal and geographic biases in recovery probabilities. In contrast, PTT data were restricted to a few individuals over a relatively short time period, but were not biased by the distribution of observer (or hunter) effort. The latter is an important consideration for Tundra Swans as recoveries and observations are more common in heavily populated areas, especially where there is a sport harvest such as in Utah.

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STATUS OF TUNDRA SWANS AND TRUMPETER SWANS IN MEXICO

RODERICK C. DREWIEN[1] AND DOUGLAS S. BENNING[2]

ABSTRACT.—We summarize Tundra Swan (*Cygnus columbianus*) and Trumpeter Swan (*C. buccinator*) observations from Mexico recorded by the U. S. Fish and Wildlife Service during January aerial waterfowl surveys, 1947–94, other winter surveys and observations, 1972–95, and band recoveries. Swans were not identified by species with certainty during aerial surveys, but were presumed to be Tundra Swans. A total of 121 swans, including five band recoveries was reported at 22 locations in seven Mexican states; 83 were in the Interior Highlands, 23 near the Gulf Coast, and 15 in Pacific Coast states. Most records were from Chihuahua (66), followed by Tamaulipas (23), Durango (13) and Sonora (11); eight were from three other states. The most commonly used winter area was Laguna de Santa Maria in northern Chihuahua where 29 swans were observed. Of 121 swans recorded, three were identified as Trumpeter Swans in Chihuahua (2) and Tamaulipas (1) and two others as possible Trumpeters in Durango. These data and information from other sources show that Tundra Swans and Trumpeter Swans are rare and irregular winter visitors, mainly to northern Mexico. *Received 25 September 1996, accepted 19 August 1997.*

The Tundra Swan (*Cygnus columbianus*) and the Trumpeter Swan (*C. buccinator*) are occasional winter visitors in Mexico. During the first half of the 20th century, Trumpeter Swans were recorded only once in Mexico, near the Gulf Coast at Matamoros, Tamaulipas in January 1909 (Phillips 1911, Coale 1915, Saunders and Saunders 1981, Howell and Webb 1995). Tundra Swans have been classified as rare to casual winter visitors to Baja California, Chihuahua, and Tamaulipas (Friedmann et al. 1950, Blake 1953, Saunders and Saunders 1981, Wilbur 1987), and currently are considered irregular, rare winter visitors to northern Mexico (Howell and Webb 1995). They were formerly more abundant in northern Mexico (Saunders and Saunders 1981) although there is little published information. Several sources (e.g., Cooke 1906, Bent 1925, Grinnell 1928, Palmer 1976, E. A. Goldman *in* Saunders and Saunders 1981:94, Saunders and Saunders 1981, Wilbur 1987) reported Tundra Swans along the Mexican Gulf Coast in Tamaulipas, the Pacific Coast in Baja California Norte and Sur, and states in the Interior Highlands, including Chihuahua, Coahuila, Durango, Guanajuato, and occasionally south to Lake Chapala, Jalisco in severe winters. In 1916, General J. Pershing's troops reported large flocks in Chihuahua at Laguna de Guzman and smaller numbers near Ascension (Saunders and Saunders 1981).

[1] Hornocker Wildlife Institute, Univ. of Idaho, P.O. Box 3246, Moscow, Idaho 83843.
[2] U.S. Fish and Wildlife Service, Office of Migratory Bird Management, P.O. Box 25486, DFC, Denver, Colorado 80225.

In this paper, we update information on the distribution and numbers of Tundra Swans and Trumpeter Swans reported in Mexico from (1) winter aerial waterfowl surveys conducted by the U.S. Fish and Wildlife Service (FWS), 1947–94, (2) other ground and aerial surveys and incidental observations, winters 1972–95, and (3) band recoveries received by the Bird Banding Laboratory.

STUDY AREAS AND METHODS

U.S. Fish and Wildlife Service aerial surveys.—We summarized the number and distribution of Tundra/Trumpeter Swans recorded by the FWS during January aerial waterfowl surveys conducted in most winters, 1947–94. The FWS initiated aerial waterfowl surveys in the Gulf and Pacific coastal states of Mexico in 1947 and in the Interior Highlands in 1951 (Saunders 1964, Saunders and Saunders 1981, Smith 1984). Other wetlands in the Interior Highlands were added to surveys through the 1960s. All swans recorded were presumed to be Tundra Swans, but due to difficulty of separating the 2 species (Banko 1960, Bellrose 1976, Patten and Heindel 1994), especially during aerial surveys, we have classified them as swans (Tundra/Trumpeter). Details of survey methods and locations, habitat conditions, and species recorded were reported by Saunders and Saunders (1981) and in Mexico Winter Waterfowl Survey Administrative Reports (filed with FWS, Off. Migr. Bird Manage., Portland, Oregon).

Areas flown by the FWS during winter waterfowl surveys in Mexico were described by Saunders and Saunders (1981), and included waterfowl habitats in three major geographical regions (Fig. 1): (1) *Gulf and Caribbean Coast Zone* (Gulf Coast) included wetlands from the Rio Grande delta along the United States–Mexico border in Tamaulipas southward to sites on the Yucatan Peninsula (see also Baldassarre et al. 1989), (2) *Interior Highlands* included the elevated central plateau from the United States–Mexico border in Chihuahua and Coahuila southward below Mexico City to Michoacan and Puebla. This region is bounded on the east by the Sierra Madre Oriental and on the west by the Sierra Madre Occidental, and (3) *Pacific Coastal Zone* (Pacific Coast) extended from Baja California and Sonora southward to Chiapas (see also Kramer and Migoya 1989).

Other surveys.—Seven wetlands in western and central Chihuahua were surveyed for waterbirds by Drewien et al. (1996). Areas from north to south included: (1) Ascension, (2) two reservoirs near N. Casas Grandes, (3) Santa Maria River valley near Galeana, (4) Laguna de Encinillas, (5) Laguna de Babicora, (6) Laguna de Bustillos, and (7) Laguna de los Mexicanos. Descriptions and locations of these wetlands were reported by Arellano and Rojas (1956), Knoder et al. (1980), Saunders and Saunders (1981), and Drewien et al. (1996).

During winters 1970 (Dec. 70–Jan. 71)–1995 (Dec. 95–Jan. 96), we made 22 trips (five aerial, 17 ground) to Chihuahua, five (four aerial, one ground) to Durango, and two (ground) to Sonora. Swans were recorded by species and age (adults—white plumage, immatures—gray plumage; Banko 1960, Limpert and Earnst 1994, Patten and Heindel 1994) during ground surveys.

We also reviewed early waterfowl surveys conducted from the ground (Goldman and Goldman 1935, 1936, Goldman 1942a,b, 1943), and report incidental observations of swans, including those by Knoder et al. (1980) during eight winter aerial surveys in the 1970s.

Band recoveries.—We reviewed band recovery data for Tundra Swans and Trumpeter Swans from Mexico to assess distribution. These data were provided by the Bird Banding Laboratory, Laurel, Maryland (J. Tautin and M. K. Klimkiewicz, pers. comm.).

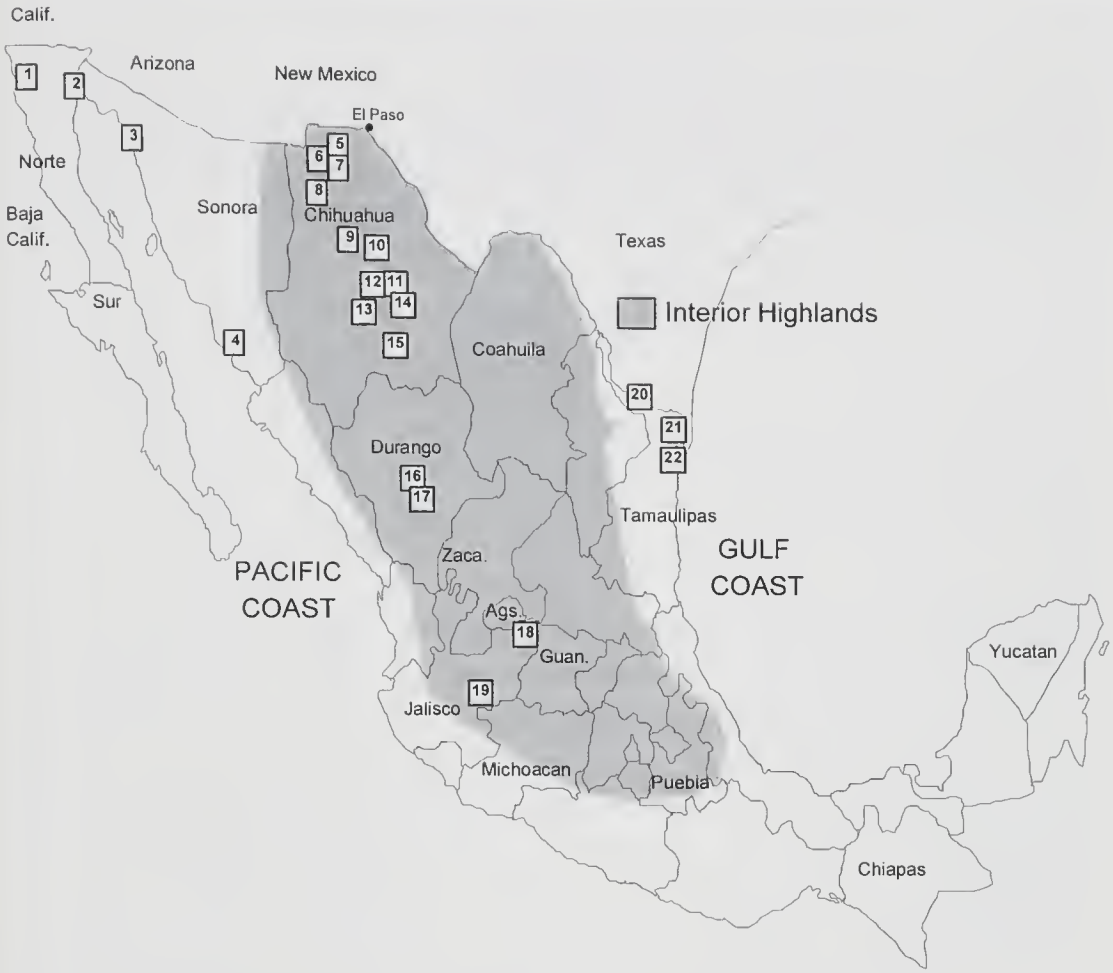

FIG. 1. Winter distribution of Tundra Swans and Trumpeter Swans in Mexico recorded by the U.S. Fish and Wildlife Service during January aerial surveys, 1947–94, Knoder et al. (1980), Drewien et al. (1996), other observers, and from band recoveries. See Table 1 for locations and numbers of swans reported.

RESULTS

U.S. Fish and Wildlife Service winter aerial surveys.—During January aerial surveys between 1947–94 (34-Gulf Coast, 27-Interior Highlands, 42-Pacific Coast), 104 swans were recorded; 70 were in the Interior Highlands, 22 along the Gulf Coast, and 12 in Pacific Coast states (Table 1). No swans were observed south of Tamaulipas along the Gulf Coast, south of Sonora on the Pacific Coast, or south of Jalisco in the Interior Highlands (Fig. 1). The southern-most sighting was of three swans in January 1975 at a wetland complex near Ocotlan, Jalisco (20°28′N, 102°47′W), north of Lake Chapala. No Mute Swans (*C. olor*) were reported during aerial surveys. Swans were recorded at 16 locations in seven states, including 11 sites in the Interior Highlands, two on the Gulf Coast, and three in Pacific Coast states (Table 1, Fig. 1). Chihuahua accounted for

TABLE 1

LOCATIONS AND NUMBERS OF TUNDRA SWANS (TUSW) AND TRUMPETER SWANS (TRSW) IN MEXICO RECORDED BY THE U.S. FISH AND WILDLIFE SERVICE (FWS) DURING JANUARY AERIAL WATERFOWL SURVEYS, 1947–94, AND OTHER OBSERVATIONS DURING WINTERS (DEC.–FEB.) 1972–95 INCLUDING FIVE BAND RECOVERIES (LOCATION NUMBERS IN FIG. 1 ARE IN BRACKETS)

Location	Number of swans			No. and date
	FWS	Other	Total	
Baja California Norte				
nr. Ensenada [1]		3	3	(3) 1987, TUSW band recoveries
northern B.C. [2]	1		1	(1) 1960[a]
Sonora				
NW Coast [3]	7		7	(7) 1980[b]
Obregon [4]	4		4	(2) 1956[c], (2) 1958
Chihuahua				
L Guzman [5]	1		1	(1) 1953
Ascension [6]		2	2	(1) 1981 TUSW[d], 1987 TRSW[d]
L. Santa Maria [7]	29		29	(4) 1951, (11) 1960, (10) 1963, 4 (1965)
N. Casas Grandes [8]		3	3	(2) 1986 TUSW[d], (1) 1992 TRSW band recovery
Tintero Res. [9]	2		2	(1) 1981, (1) 1991
L. Encinillas [10]	2	2	4	(2) 1979, (2) 1986 TUSW[d]
Chihuahua City [11]		2	2	(2) 1995 TUSW[e]
L. Bustillos [12]	6		6	(3) 1975, (2) 1979, (1) 1981
L. Mexicanos [13]	8	1	9	(1) 1976 TUSW[d], (5) 1979, (3) 1988
L. Delicias [14]		1	1	(1) 1972 TUSW band recovery
L. Toronto [15]	7		7	(3) 1955, (3) 1975, (1) 1982
Durango				
L. Santiaguillo [16]	8	2	10	(2) 1979 TRSW[f], (7) 1985, (1) 1988
Durango [17]	3		3	(1) 1982, (2) 1985
Aguascalientes-Jalisco border				
El Languillo [18]	1		1	(1) 1980
Jalisco				
Ocotlan [19]	3		3	(3) 1975
Tamaulipas				
Falcon Dam [20]		1	1	(1) 1989 TRSW[g]
Rio Grande delta [21]	10		10	(10) 1977
Laguna Madre [22]	12		12	(11) 1964, (1) 1975
Total	104	17	121	

[a] Saunders and Saunders (1981:94) reported sighting for 1959, but records show 1960, specific location not given.
[b] Specific location not recorded.
[c] Saunders and Saunders (1981:94) reported this sighting in Baja California but records show they were in Sonora.
[d] Recorded during surveys by Drewien et al. (1996).
[e] Reported by R. Uranga T., Chihuahua, Chih. (pers. comm.)
[f] Recorded during surveys by Knoder et al. (1980).
[g] Reported by H. H. Burgess, Weslaco, Texas (pers. comm.).

52.9% (55) of the swans recorded, Tamaulipas 21.2% (22), Durango 10.6% (11), Sonora 10.6% (11), and the remaining 4.8% (5) were found in three other states. The most commonly used winter site was Laguna de Santa Maria, Chihuahua where 29 swans (27.9%) were observed. Classification of 29 groups and single swans recorded showed that singles (10) and pairs (5) accounted for 51.7% of sightings, flocks of 3-7 (10) 34.5%, and flocks of 10-11 (4) 13.8% (Table 1). Numbers of swans observed by decade were: 1940s-0, 1950s-13; 1960s-36; 1970s-29; 1980s-25; 1990s-1.

Other surveys.—Seven swans, including six Tundra Swans (five adults, one immature) and a probable immature Trumpeter Swan classified by its very dark juvenal plumage (Patten and Heindel 1994) were recorded at four locations in Chihuahua during surveys by Drewien et al. (1996) (Table 1). FWS aerial surveys had not previously recorded swans at two of these locations. Knoder et al. (1980, C. E. Knoder pers. comm.) saw 2 adults at Laguna de Santiaguillo, Durango on 28 February 1979 (Table 1), and based upon their size, no obvious yellow lore spots and behavior suspected that they were Trumpeters. An immature Trumpeter Swan wintered along the international border in both Tamaulipas and Texas on the Rio Grande below Falcon Dam during 1989/90 (H. H. Burgess, pers. comm.). Two Tundra Swans were observed (1 immature photographed) northeast of the city of Chihuahua in January 1995 (R. Uranga T., Chihuahua, Chih., pers comm.). These sightings involved single swans or pairs (Table 1). No swans were observed during ground surveys in the 1930s–early 1940s, although Goldman (1942a,b) reported swan sightings during earlier years at Laguna de Encinillas and Laguna de Babicora, Chihuahua.

Band recoveries.—Recoveries of Four Tundra and one Trumpeter Swan from Mexico were reported to the Bird Banding Laboratory through October 1995 (Table 1, Fig. 1). Three immature Tundra Swans were recovered near Ensenada in northwestern Baja California Norte in December 1987. They had been banded at Izembek National Wildlife Refuge, Alaska, during July 1987, and possibly were a family group. Another Tundra Swan, an immature banded near the Selawik River, Alaska by W. Sladen in August 1972, was reported near Delicias, Chihuahua in December 1972. An adult female Trumpeter Swan that was shot at N. Casas Grandes, Chihuahua in December 1992, had been banded by the first author on the Henry's Fork of the Snake River, Fremont County, Idaho in November 1992 and translocated with 37 other Trumpeter Swans to the Seedskadee National Wildlife Refuge, Sweetwater County, Wyoming. Of the five recoveries, three were misidentified as geese and shot, one was found with a broken wing, and one was an observation of a neck-collared swan.

DISCUSSION

The FWS aerial surveys, other surveys and observations, and band recoveries confirm that Tundra Swans and Trumpeter Swans are rare and irregular winter visitors mainly to northern Mexico. Swans were recorded at 22 locations in seven states with most records confined to the northern border states (86%) of Chihuahua, Tamaulipas, Sonora, and Baja California Norte; a few swans were observed southward in the Interior Highlands (14%) in Durango, Aguascalientes, and Jalisco.

The FWS winter waterfowl surveys probably identified the more important wetlands occasionally visited by swans in Mexico except in Baja California. Aerial surveys in Baja California focused mainly on coastal habitats used by Brant (*Branta bernicla*) and the Colorado River delta, and did not include other inland water areas where swans might occur. Wilbur (1987:53) noted that Tundra Swans were "Irregular winter visitors, a few apparently reaching Baja California almost every year." FWS surveys also recorded 11 swans at two sites in Sonora although none were reported by van Rossem (1945).

The largest number (29) of swans was observed at Laguna de Santa Maria, in northern Chihuahua between 1951–65; none has been observed there since 1965. Laguna de Santa Maria and the adjacent Laguna de Guzman are shallow lakes formed in sinks of the Casas Grandes and Santa Maria rivers. Although formerly they were important winter sites for waterfowl and cranes (Goldman 1942b, Saunders and Saunders 1981), the habitat quality of wetlands in the Interior Highlands has declined dramatically during this century due to upstream water diversions, drought cycles and human impacts (Corzo 1970, Saunders and Saunders 1981). In 1899, E. A. Goldman (1951:123) described Laguna de Santa Maria as "a saline body of water about 8 miles long and 6 miles wide . . . separated from that of the Laguna de Guzman . . . a short distance to the northwest, by a divide not more than 200 feet high. . . . Cottonwoods, willows, and mesquites grow along the Rio Santa Maria." In contrast, the January 1965 FWS survey report described Santa Maria as: "A small spring-fed reservoir remained with only a few acres of overflow water . . . in the sump adjoining." (Saunders and Saunders 1981:36). Only small numbers of geese and ducks averaging 1230, have been recorded there during 13 FWS winter surveys since 1965.

Currently, over 99% of Tundra Swans typically winter in traditional areas in the Pacific and Atlantic Flyways and only small numbers winter in the interior of the United States (Bellrose 1976, Serie and Bartonek 1991). Midwinter (January) counts compiled by the FWS since the mid-1950s show that Tundra Swans have been increasing (Serie and Bartonek

1991, Limpert and Earnst 1994), but not in the south-central United States near Mexico where they were formerly more common (Oberholser 1974). During Januarys 1990–96, the Western Population in the Pacific Flyway averaged 63,400 (Bartonek 1995, Trost 1996) and the Eastern Population in the Atlantic Flyway averaged 88,000, whereas an average of 590 wintered in the Mississippi Flyway and only eight in the Central Flyway (Sharp 1996).

Trumpeter Swans, formerly abundant and widespread in North America, were extirpated over most of their range by 1900 (Coale 1915, Bent 1925, Banko 1960). During recent decades they have increased (Mitchell 1994, Gillette and Shea 1995). A 1995 continental survey accounted for 19,756 with over 16,300 in Alaska and northwestern Canada (Caithamer 1996). Historically, their winter range included the Gulf Coast to Tamaulipas and adjacent interior areas in the southern United States (Banko 1960, Banko and Mackay 1964, Oberholser 1974). Their diminished abundance, the difficulty of distinguishing them from Tundra Swans (Banko 1960, Bellrose 1976, Pattern and Heindel 1994), and the rarity of swans in Mexico, have all contributed to the paucity of Trumpeter Swan records from Mexico during this century.

While Tundra and Trumpeter Swan populations have increased in North America during recent decades, these increases have not been reflected in more swans wintering in Mexico. Swans can only be expected to increase in Mexico if mortality of pioneers is minimized and suitable wetland habitats are conserved and enhanced.

ACKNOWLEDGMENTS

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THE SUMMER DIET OF THE YELLOW RAIL IN SOUTHERN QUÉBEC

MICHEL ROBERT,[1] LOUISE CLOUTIER,[2] AND PIERRE LAPORTE[1]

ABSTRACT.—We documented Yellow Rail (*Coturnicops noveboracensis*) food habits through the use of tartar emetic, a non-destructive method to collect stomach contents. A total of 71 rails were forced to regurgitate during 9 Jun.–25 Aug. 1994 and 16 May–31 Jul. 1995, from which we obtained 105 emetic samples. Almost 95% (99/105) of samples contained food items. Overall, mean number of taxa within one sample was 4.7 (SD = 3.2; Range = 1–13; N = 99): 1.1 (SD = 1.6; Range = 0-7) for seeds and 3.6 (SD = 2.1; Range = 0–8) for invertebrates. Sand grit, feather fragments, and plant fragments were also identified in many samples. Totals of 1169 organisms from 52 taxa were identified and counted in the samples: 372 seeds from 18 taxa and 797 invertebrates from 34 taxa. Invertebrates and seeds had relative frequencies of 68.1% and 31.9%, respectively, and the mean number of individuals counted within samples was significantly higher ($P < 0.001$) for invertebrates (Mean = 8.1; SE = 0.8; Range = 0–44) than for seeds (Mean = 3.8; SE = 0.9; Range = 0–44). Among the first group, Coleoptera (beetles) were by far the most important food, representing almost two-thirds of invertebrates eaten and having a relative frequency of 42.5%. Araneae (spiders) were second, with a relative frequency of 13.3%, while other taxa ranked far lower. Of seeds identified, Cyperaceae (sedges) and Juncaceae (rushes), particularly genera such as *Carex*, *Juncus*, and *Eleocharis*, were the most important food items, with relative frequencies of 12.7%, 6.5%, and 3.1%, respectively. According to our results, during summer the Yellow Rail is mostly an arthropod-feeder that complements its diet with seeds. Effects of tartar emetic on birds were negligible and this technique appeared to be very successful, suggesting that it could be used as an alternative to sacrificing rails in future dietary studies. *Received 30 Oct. 1996, accepted May 1997.*

The Yellow Rail (*Coturnicops noveboracensis*) is one of North America's least studied birds (Bookhout 1995, Robert 1997). Many reports state that snails are the principal food taken by this bird (Peabody in Bent 1926, Walkinshaw 1939, Stalheim 1974:8, Ripley 1977, Bookhout 1995). Only Martin et al. (1951), Easterla (1962), Stalheim (1974), and Martin and Perry (1981) published quantitative information on the diet of wild-caught Yellow Rails, and their results refer to only 20 or so individuals, many of which were collected during migration or in winter. Moreover, a portion of their gizzard contents was not consistently preserved in alcohol, which brings into question the reliability of some results (Stalheim 1974). Other publications dealing with the food habits of Yellow Rails either refer to captive birds (Devitt 1939, Stalheim 1975) or are too gen-

[1] Canadian Wildlife Service, Québec Region, Environment Canada, 1141 route de l'Église, C. P. 10100, Sainte-Foy, Québec, Canada GIV 4H5.
[2] Univ. de Montréal, Collection Ouellet-Robert, Dépt. de sciences biologiques, C. P. 6128, succursale Centre-Ville, Montréal, Québec, Canada H3C 3J7.

eral or anecdotal to present a clear picture of the bird's diet (Wayne 1905, Walkinshaw 1939, Huber 1960).

In Québec, as in some other parts of North America (Bookhout 1995), the Yellow Rail is considered to be a vulnerable species because of its rarity and the fragility of its habitat (Robert 1996). As part of our ongoing investigations of threatened birds in Québec, we captured and banded Yellow Rails (Robert and Laporte 1997) and subsequently took advantage of this opportunity to document food habits of this species using tartar emetic, a non-destructive method to collect stomach contents. In this paper, we present and discuss quantitative analysis of foods taken by Yellow Rails during summer. We also present fresh weights of the rails caught and discuss their weight variations in relation to tartar emetic use.

STUDY AREA AND METHODS

In 1994 and 1995, we banded Yellow Rails in marshes along the St. Lawrence River. From southwest to northeast along the St. Lawrence corridor, we worked in the Lac Saint-François (45°02′N, 74°32′W) and Cap Tourmente (47°03′N, 70°49′ W) National Wildlife Areas (NWA), at Île aux Grues (47°04′N, 70°33′W), Cacouna (47°56′N, 69°31′W), and at Gaspé Bay (48°50′N, 64°29′W). The salinity of the St. Lawrence River varies depending on location: the water is fresh in Lac Saint-François, brackish at Cap Tourmente and Île aux Grues, and salty at the other sites. The vegetation of these marshes is low herbaceous graminoids (<1 m high), chiefly sedges (Cyperaceae), rushes (Juncaceae) and true grasses (Gramineae) (Robert and Laporte 1996).

All rails were caught at night (22:30–03:30, DST) from mid-May to late August, with techniques described in Robert and Laporte (1997). Rails were weighed to the nearest gram using a 100-g Pesola scale and sexed according to bill color; during the breeding season, males have a yellowish bill and females a much darker one (Walkinshaw 1939, Stalheim 1974). They were forced to regurgitate by orally administering to them a 1.5% solution of antimony potassium tartrate (tartar emetic) according to the method of Poulin et al. (1994), but at a dosage increased from 0.8 cm^3 to 0.9 cm^3 per 100 g of body mass. We used a small, 6-cm feeding tube (gauge 8 FR) attached to a 1-cm^3 syringe to inject the solution. The emetic was administered slowly, over a two minute period, waiting for the bird to swallow and recover whenever necessary. Once the emetic was given, the rail was placed in a small dark box lined with white cotton fabric and was released 15–20 min later after having regurgitated and recovered. All food items were then immediately transferred to glycerinated 70% ethanol.

All items found in samples were identified in the laboratory by one person (LC), using a dissecting microscope. They were first classified into sand grit, feathers, plants, Gastropoda, seeds, or Arthropoda. For each sample, grains of sand and feather rachis fragments were individually counted, while plants, which were too much fragmented to be identified, were quantified using a semi-quantitative relative abundance scale: 0 (no plant), 1 (small quantity), 2 (medium quantity), and 3 (large quantity). For each sample, Gastropoda were individually counted using shell apex, while seeds and Arthropoda were specifically counted and identified using reference collections of species found in studied habitats. Nearly all Arthropoda were highly digested and fragmented, and their identification was based on the most characteristic and least digestible parts of their body. They were classified and counted,

using chelicerae for Araneae, metasomatic segments for Hymenoptera, elytra base for Coleoptera, and head parts or wings for other taxa.

We calculated the overall mean number of food types counted in gizzard contents for samples containing food, as well as the frequency of occurrence for all food types within samples. We also calculated the relative frequency for all seeds and invertebrates i.e., the number of individuals in each taxon as a proportion of the total individuals in all taxa, expressed in percentage. Using Kruskal-Wallis tests, we tested differences in mean numbers of seeds and invertebrates in samples collected at Île aux Grues, Lac Saint-François NWA, and Cacouna. We also tested, from data collected at Île aux Grues, for the significance of a possible association between sample collection dates and number of predominant food types using Kendall's coefficient of rank correlation. We used a Wilcoxon test to compare the number of seeds and the number of invertebrates counted within samples, as well as a paired *t*-test to compare the mean weight of rails before and after the treatment with the emetic solution.

RESULTS

A total of 71 Yellow Rails were forced to regurgitate during 9 Jun–25 Aug. 1994 and 16 May–31 Jul. 1995, from which we obtained 105 samples. Almost 95% of samples (99/105) contained recognizable food items, while six were strictly liquid. Most rails regurgitated once (N = 46), but some were recaptured and forced to regurgitate a second (N = 18), third (N = 5), and fourth (N = 2) time during a given year. More than three-quarters of samples (76/99) containing recognizable food were obtained at Île aux Grues, 10 at Lac Saint-François NWA, nine at Cacouna, three in Gaspé Bay, and one at Cap Tourmente NWA. Up to and including the time of release, neither mortality nor discernable weakness was observed in the captured rails; many birds (26/71) were recaptured after having been treated with the emetic.

Overall, the mean number of taxa identified within one sample was 4.7 (SD = 3.2; range = 1-13; N = 99): 1.1 (SD = 1.6; range = 0-7) for seeds and 3.6 (SD = 2.1; range = 0-8) for invertebrates. Moreover, sand grit, feather fragments, and plant fragments were identified in many samples. Feather and plant fragments (mostly dead vegetation) were present in most samples but usually not in large quantities (Table 1). Overall, a total of 1169 organisms from 52 taxa were identified and counted in all samples; 372 seeds from 18 taxa and 797 invertebrates from 34 taxa. Among seeds, Cyperaceae (*Carex hormatodes, C. paleacea, C. echinata, Carex* sp., and *Eleocharis* sp.) and Juncaceae (*Juncus balticus*) were the most represented families, with 49.5% and 20.4% of all seeds counted, respectively. These, along with Graminaeae (*Spartina pectinata* and/or *Calamagrostis canadensis* and/or *Festuca rubra*) and Lythraceae (*Lythrum salicaria*) had the highest frequencies of occurrence (Table 1) and were also either dominant or co-dominant in the marshes studied (Robert and Laporte 1996). Except for at least eight taxa that could not be iden-

TABLE 1

SUMMER FOOD TYPES FOUND IN EMETIC SAMPLES (N = 99) OF YELLOW RAILS FROM SOUTHERN QUÉBEC

	Number of taxa identified (minimum)	Number of indiv. counted	Mean number indiv./ sample	Maximum number indiv./ sample	Frequency of occurrence	Relative frequency
Seeds	**18**	**372**	**7.8**	**44**	**48.5**	**31.9**
Polygonaceae	1	7	3.5	6	2.0	0.6
Lythraceae	1	13	1.6	5	8.1	1.1
Rubiaceae	1	10	1.7	5	6.1	0.9
Juncaginaceae	1	2	1.0	1	2.0	0.2
Juncaceae	1	76	7.6	24	10.1	6.5
Cyperaceae	4	184	5.6	38	33.3	15.7
Gramineae	1	22	2.0	6	11.1	1.9
Unidentified	8	58	2.8	26	21.2	5.0
Invertebrates	**34**	**797**	**9.1**	**44**	**90.9**	**68.1**
Gastropoda	1	55	1.5	6	37.4	4.7
Hirudinea	1	2	2.0	2	1.0	0.2
Acarina	1	4	1.0	1	4.0	0.3
Araneae	1	156	2.7	10	57.6	13.3
Collembola	1	7	1.2	2	6.1	0.6
Psocoptera	1	6	2.0	3	3.0	0.5
Mallophaga	1	1	1.0	1	1.0	0.1
Hemiptera	1	1	1.0	1	1.0	0.1
Homoptera	1	5	1.0	1	5.1	0.4
Thysanoptera	1	1	1.0	1	1.0	0.1
Coleoptera	14	497	7.0	41	71.7	42.5
Trichoptera	1	1	1.0	1	1.0	0.1
Hymenoptera	1	4	2.0	3	2.0	0.3
Diptera	7	53	2.2	10	24.2	4.5
Diptera pupae	1	2	1.0	1	2.0	0.2
Others	**—**	**—**	**—**	**—**	**79.8**	**—**
Sand grit	—	33	2.8	19	12.1	—
Feather fragments	—	297	5.1	23	58.6	—
Plant fragments	—	—	—[a]	—	67.7	—

[a] Frequency distribution of semi-quantitative classes: 0 = 32.3%, 1 = 25.3%, 2 = 30.3%, 3 = 12.1%.

tified, the remaining seeds found in the samples were from Polygonaceae (*Polygonum* sp.), Rubiaceae (*Galium* sp.), and Juncaginaceae (*Triglochin maritima*) families.

Among invertebrates, the most common food items were Coleoptera, Araneae, Gastropoda, and Diptera, with 62.4%, 19.6%, 6.9% and 6.6% of all animals counted, respectively (Table 1). Many Coleoptera and Diptera families were identified. They were, in decreasing importance: Hy-

drophilidae (*Helophorus* sp. and *Cymbiodyta vindicata*), Curculionidae (*Listronotus* sp. and ≥2 unidentified spp.), Carabidae (*Poecilus* and/or *Pterostichus* and/or *Harpalus* and/or *Patrobus* genera), and Sylphidae (*Thanatophilus lapponicus*) for Coleoptera, and Chironomidae (≥1 sp.), Ceratopogonidae (≥1 sp.), Culicidae (≥1 sp.), Dolichopodidae (≥1 sp.), Tipulidae (*Dicranota* sp.), and Simuliidae (≥1 sp.) for Diptera. At least eight more taxa, seven Coleoptera and one Diptera that could not be identified, were found in the samples. Other invertebrates identified, in decreasing relative frequencies and frequencies of occurrence, were insects from Collembola (≥1 sp.), Homoptera (≥1 sp.), Psocoptera (≥1 sp.), Hymenoptera (≥1 Formicidae), Mallophaga (≥1 sp.), Hemiptera (≥1 Corixidae), Thysanoptera (≥1 sp.), and Trichoptera (≥1 sp.) orders, as well as Acarina (≥1 sp.) and Hirudinea (≥1 sp.) (Table 1).

Overall, invertebrates and seeds had relative frequencies of 68.1% and 31.9% respectively, while the overall mean number of individuals counted within samples was significantly higher (Wilcoxon test, $\chi^2 = 40.8$, $P < 0.001$) for invertebrates (Mean = 8.1; SE = 0.8; range = 0–44; N = 99) than for seeds (Mean = 3.8; SE = 0.9; range = 0–44; N = 99). Among the first group, Coleoptera was by far the most important food taxon, representing almost two-thirds of invertebrates eaten and having a relative frequency of 42.5%. Hydrophilidae and Curculionidae had particularly high relative frequencies among Coleoptera: 19.3% and 13.4% respectively. The taxon Araneae was second among invertebrates, with a relative frequency of 13.3%, while other taxa followed far behind. Among the latter taxa, Diptera and Gastropoda had relative frequencies less than 5.0% (Table 1). Cyperaceae and Juncaceae, particularly the genera *Carex, Juncus*, and *Eleocharis*, were the most important food items among seeds with relative frequencies of 12.7%, 6.5% and 3.1%, respectively.

We did not find any significant differences (Kruskal-Wallis test, $P > 0.05$) between mean numbers of seeds and invertebrates counted in samples collected at Île aux Grues, Lac Saint-François NWA and Cacouna. We did not find significant correlations (Kendall statistics, $P > 0.05$) between collection dates and numbers of seeds, invertebrates, Coleoptera or Cyperaceae counted in samples collected at Île aux Grues, although there was a significant negative relationship between the numbers of Araneae found in samples and collection dates (Kendall's Tau = −0.18, $P = 0.04$).

All rails had a predominantly yellow bill and were considered as males. Their mean weight was 60.9 g (N = 71; SD = 3.5; range = 53–70 g). The mean weight of birds forced to regurgitate did not vary significantly before they were treated with tartar emetic and after they were recaptured (two-sided paired *t*-test, $P = 0.52$, N = 36).

DISCUSSION

This study represent the first exhaustive report of summer food habits of Yellow Rails. Our results indicate that this species feeds on a wide variety of resources, including both animal and vegetal matter in its diet. This reflects an opportunistic foraging strategy which contrasts with statements closely associating Yellow Rails and snails. Not only was the number of food taxa found in our samples generally high, but also the relative importance of snails in our samples appeared to be fairly low (although snails were numerous in all studied habitats). According to our data, the Yellow Rail, during summer, is predominantly an arthropod-feeder that complements its diet with seeds. This is in agreement with Stalheim's (1974) statement that although seeds may at times comprise a large part of its diet, invertebrates appear to be a regular and important feature. He also noted that the Yellow Rail's gizzard is anatomically more similar to that of the Virginia Rail (*Rallus limicola*) than to that of the Sora (*Porzana carolina*), and because Virginia Rails consume a much higher percentage of animal foods than do sympatric Soras (Horak 1970, Conway 1995), he suggested that Yellow Rails may be more adapted to a diet of invertebrates than to a diet of seeds. The low incidence of sand grit in our samples corroborates Stalheim's (1974) suggestion; the quantities found in this study are similar to those measured in the invertebrate-eating Virginia Rails, which are much lower than those measured in seed-eating birds such as Soras (Horak 1970).

No published information had clearly shown the relative importance of animal matter in the diet of the Yellow Rail. Many invertebrate taxa were identified by Martin et al. (1951), Easterla (1962), and Stalheim (1974), but the minute quantities found in the gizzards they analysed did not permit numerical estimations. However, traces of Gastropoda, Pelecypoda, Arachnida, Crustacea, Orthoptera, Hemiptera, Coleoptera, Diptera, and Hymenoptera were identified in their samples. Other information on invertebrates being eaten by Yellow Rails is extremely rare: Diplopoda (millipedes) made up 23% of the gizzard volume for one bird collected in Missouri (see Stalheim 1974), Tettigonidae (grasshoppers) and Amnicolidae (snails) made up 40% and 25%, respectively, of the gizzard volume for one rail shot in Maryland (Martin and Perry 1981), while snails made up 90% of the gizzard volume for one bird collected in Massachusetts (Martin and Perry 1981). Seeds made up a major part of the gizzard contents of Yellow Rails collected to date and a few plant taxa were identified, including *Acalypha virginica, Ambrosia* sp., *Carex* sp., *Eleocharis* sp., *Myrica* sp., *Polygonum* sp., *Rosa* sp., *Scirpus acutus, Scleria* sp., *Setaria glauca*, and *Viola sagittata* (Stalheim 1974, Martin and Perry

1981). Although we can infer that seeds may sometimes make up a large part of the diet of individual birds, even in summer (Easterla 1962, Stalheim 1974, this study), it is likely that the relative importance of seeds was overestimated in most of previous studies because the gizzards were not preserved soon after bird's deaths and seeds take longer to digest than soft-bodied arthropods (Stalheim 1974). Moreover, most of previous studies samples were taken from Yellow Rails collected during migration or during winter, when a bird's diet may differ considerably from its summer food. For instance, Martin et al. (1951) showed that Virginia Rails do consume seeds more commonly in fall (32%), winter (21%), and spring (12%) than in summer (3%), which could also be the case for Yellow Rails (see also Meanley 1992).

Many of the animal and plant taxa found in our samples had never been reported in the Yellow Rail diet studies. These include Hirudinea (leeches) and two individuals were actually found in the gizzard contents of one rail caught at Île aux Grues. It seems that leeches are rarely preyed upon by rallids (see Bent 1926, Martin et al. 1951, Ohmart and Tomlinson 1977, Cramp 1980), which our results tend to corroborate. In our view, it is likely that leeches are taken by Yellow Rails mainly because they sometimes are parasitized by these annellids: during our study, four of the Yellow Rails we caught had a leech attached to its toe or tarsus. Other food taxa reported for the first time within this study are seeds from Lythraceae, Rubiaceae, and Juncaginaceae families and invertebrates from Acarina, Collembola, Psocoptera, Mallophaga, Homoptera, Thysanoptera, and Trichoptera orders.

Although nearly all samples contained food items and although the overall mean number of food types found within one sample was fairly high, most samples were made up of only a few highly digested items. This suggests that the gizzard of many rails was mainly empty when we forced them to regurgitate, which could be due to the fact that the birds were always caught at night (Robert and Laporte 1997). Stalheim (1974), who studied semi-captive Yellow Rails, did not observe feeding during night-time in spite of regular night observation, but observed birds feeding from sunrise to nearly sunset. Telemetric studies (Bookhout and Stenzel 1987, Robert and Laporte 1996) also showed that Yellow Rails are sedentary at night and mobile during the day. In our view, the small quantities of food found in our samples corroborate Stalheim's observation, i.e., that the Yellow Rail is a daytime feeder. Thus, it is likely that our results underestimate prey items with higher digestability such as small soft-bodied arthropods, eggs, insect larvae, and worms (see Swanson and Bartonek 1970). Inversely, our results probably slightly overestimate the relative importance of hard-bodied food items, particularly

seeds, and probably beetles and snails also. Although quite exceptional, it is worth reporting that we once observed a Yellow Rail capturing and eating two mosquitoes (Diptera, Culicidae) after it was released from banding i.e., during the night.

There are no previous reports on emetics being used with rallids (Poulin et al. 1994, Poulin and Lefebvre 1995). According to our experience, tartar emetic was a successful technique for the investigation of food preference in Yellow Rails; only 5.7% of the birds failed to regurgitate food items and several invertebrate and plant taxa were found in our samples. Furthermore, rails that were manipulated showed no sign of illness when released, and no significant differences were found between pre-treatment and post-treatment weights, suggesting that post-release effects of tartar emetic were negligible, if not non-existent (see also Poulin and Lefebvre 1995). Before beginning our study on Yellow Rails, we also tested tartar emetic with Virginia Rails on three occasions, and always had positive results. In our view, this technique could be used as an alternative to sacrificing rallids in future dietary studies, particularly for those taxa considered rare, endangered or threatened (see Eddleman et al. 1988).

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MALE MORPHOLOGY AND NEST-SITE QUALITY IN HOUSE SPARROWS

REBECCA T. KIMBALL[1]

ABSTRACT.—Previous research on House Sparrows (*Passer domesticus*) in Europe indicated that males with larger bibs are more likely to obtain nest sites with multiple potential nests. To test this observation experimentally, I created nest sites containing either one or two nest boxes. I found no morphological differences, including bib size, between males at single-box nest sites (SBNS's) and those at double-box nest sites (DBNS's). Pairs in DBNS's were more likely to renest than pairs in SBNS's in 1992, leading to increased seasonal reproductive success for pairs at DBNS's. Although pairs at DBNS's fledged more young over the season, I could not detect a strong preference for DBNS's. Pairs in DBNS's did not begin reproducing prior to those in SBNS's, as might be expected if birds preferentially occupied DBNS's prior to SBNS's. More DBNS's than SBNS's were occupied in 1991, but this was not true in 1992 when sample sizes were larger. *Received 2 Dec. 1996, Accepted 11 May 1997.*

Multiple nest sites on a territory may be beneficial, possibly allowing pairs to choose the best site for nesting, to renest in a clean site free of ectoparasites, or to reduce the interval between broods (Møller 1993, Meek and Robertson 1994). Experimental manipulation of the number of nest boxes on a territory indicates that Eastern Bluebirds (*Sialia sialis*) are more likely to occupy or respond from territories with multiple nest boxes (Meek and Robertson 1994, Plissner and Gowaty 1995). If multiple nest sites are beneficial, then dominant or high quality males should be more likely to occupy territories with multiple cavities than will subordinate or low quality males, and females should prefer to nest with males holding territories with multiple cavities.

House Sparrows are facultative cavity nesters and will utilize nest boxes, as well as construct open nests. Cavity nest sites are preferred to sites with no cavities (Cink 1976, Møller 1988). Pairs that nest in cavities or nest boxes have greater reproductive success (Cink 1976, McGillivray 1981), in part because these nests are less likely to be destroyed during storms (Møller 1988). In Europe, bib size is under sexual selection, with large-bibbed males being dominant (Møller 1987a, b), being preferred by females (Møller 1988) and having greater reproductive success (Møller 1988). Large-bibbed males are more likely to obtain nest sites with multiple cavities (Møller 1988), and males with experimentally enlarged bibs occupied nest sites with more nest boxes than did control males (Veiga 1993). House Sparrows may switch nest boxes between nesting attempts

[1] Dept. of Biology, The Univ. of New Mexico, Albuquerque, New Mexico 87131.

within a season (Naik and Mistry 1980), so multiple cavities within a nest site may allow pairs to renest without incurring the costs associated with locating and defending a new nesting site.

I manipulated nest site quality in a population of House Sparrows by placing either one or two nest boxes on a tree. Since I expected nest sites with two nest boxes to be preferred, I determined whether males occupying double-box nest sites (DBNS's) had larger bibs or exhibited other morphological differences as compared with males at single-box nest sites (SBNS's). Since multiple nest boxes may be beneficial, I expected that pairs at DBNS's would have greater reproductive success than pairs at SBNS's. I also expected that pairs at DBNS's would begin breeding prior to pairs at SBNS's and that more DBNS's than SBNS's would be occupied.

METHODS

I mistnetted House Sparrows in the spring of 1991 and 1992 and banded them with a unique combination of leg bands—one aluminum Fish and Wildlife Service band and two plastic color bands. I measured wing chords (unflattened), tarsi lengths, bill lengths, and bill depths. I photographed males and digitized the photos. Bib areas were measured using NIH Image (developed at the U.S. National Institutes of Health, available by anonymous FTP from zippy.nimh.nih.gov). I included a ruler in each photograph to convert measurements to mm^2. Sample sizes for the male morphology data were large enough for analysis only in 1992.

To manipulate nest site quality, I placed either one or two nest boxes on the bole of a tree on the Univ. of New Mexico campus, Albuquerque, New Mexico. Trees with nest boxes were clustered in a few areas on campus. This meant that nest box trees were never more than 28 m from another nest box tree, with most trees being no more than 10–16 m away from another nest box tree. Many of these trees contained previously used natural nests, so the dispersion of the nest boxes should have been similar to that of House Sparrow nests in natural nest sites in this area. Birds may have considered both natural nest sites and nest box sites when assessing nest site quality. However, all natural nest sites I observed in these trees were much higher than nest boxes, and were generally on lateral branches away from the bole. Given the small nest sites defended by sparrows, it is unlikely that natural and box nest sites would be considered simultaneously. In addition, after nest boxes were erected, I observed only one natural nest elsewhere in a nest box tree, suggesting that the sparrows focused on nest boxes once they were available.

Nest boxes were 11.4 × 11.4 × 22.9 cm and had a hinged door to allow access to the nest. The hole was 3.8 cm in diameter which prevented use of the boxes by European Starlings (*Sturnus vulgaris*), the only other cavity nesting species in the area. I placed nest boxes 3.0 to 3.7 m above the ground, a height suitable for House Sparrows (Weaver 1939, North 1973). This also ensured that humans could access the boxes only by use of a ladder. To prevent overheating of the nest contents, I placed nest boxes on the north sides of the trees with the hole facing north.

For DBNS's, I placed one box directly above the other so that the entrances to the two boxes were between 23 and 25 cm apart. This close proximity allowed the two boxes to be defended by one male. At no time during the two years did I observe two males simultaneously occupying a single DBNS. Males utilized the roofs of the nest boxes for display,

always displaying from the top nest box in DBNS's. However, when nesting in DBNS's, there did not appear to be a preference for top or bottom boxes, with many pairs using both boxes within a season. I created 20 SBNS's and 20 DBNS's in January 1991. An additional 20 SBNS's and 20 DBNS's were created in January 1992 for a total of 80 nest sites in 1992.

In 1991, I checked nest box contents after external signs of occupancy, such as nesting material, were detected. Occupied boxes were then checked every two to three days until the young were banded at 10 to 12 days of age. After all nesting had ceased in 1991, I removed nest material from all nest boxes which had been used and sprayed them with an insecticide (0.1% pyrethrin flea and tick spray). In 1992, all nest boxes were checked weekly beginning in March. Once an egg had been laid, the nest box was checked every other day until the young were banded. After banding the young, at 10 to 12 days of age, nests were left undisturbed for two weeks before being checked again. If the nest was abandoned directly after I disturbed the female while she sat on the nest, the nest was deleted from analyses.

I recorded the date, number of eggs laid, number hatched, and number of young banded (referred to as the number of young fledged). Juveniles were weighed with a 50 g Pesola scale at this time.

Due to the high population density and the large number of nest sites, I could not always determine the date when a nest site became occupied or a male obtained a mate. However, when I observed that a male had obtained a mate, nest building and egg laying always followed rapidly. In this population, pairs which began reproducing earlier had higher reproductive success (Kimball 1995), so it is unlikely that pairs delayed breeding once pairing occurred. Therefore, I used date of the first egg laid as a relative estimate of when a male attracted a mate to his territory.

Variables which were not normally distributed, as determined by a Shapiro-Wilks test, were analyzed using non-parametric statistics, as indicated in the results. Since I expected that DBNS's would be occupied by large-bibbed males, would have greater reproductive success, and would be preferred, I used one-tailed tests for all comparisons between SBNS's and DBNS's. Pairs which nested in both a SBNS and a DBNS in the same season were deleted from these analyses. Power analyses were performed using GPOWER (Faul and Erdfelder 1992). Power analysis depends upon estimating the effect size or the expected relative difference between two means (Cohen 1969). Since it is difficult to estimate effect size, I report power results for both a small ($d = 0.2$) and a large ($d = 0.8$) effect size (Cohen 1969).

The data from 1991 and 1992 differed in several respects (Table 1). Therefore, I analyzed data from the two years separately.

RESULTS

Male bib size did not differ between males occupying DBNS's and those at SBNS's (Table 2), contrary to my expectations. The power of the tests was low ($power_{d=0.2} = 0.11$; $power_{d=0.8} = 0.43$), so I could not conclusively accept the null hypothesis that bib size is the same between males at SBNS's and those at DBNS's. However, the difference in mean bib size between the two types of nest sites was small (18 mm^2, Table 2), particularly considering the variability of bib sizes I observed in this study ($\bar{x} = 387.1$ mm^2, SD = 139.3 mm^2, range = 175.3–589.7 mm^2).

TABLE 1

DIFFERENCES IN REPRODUCTIVE SUCCESS BETWEEN 1991 AND 1992

Variable	1991	1992	z or t (df)	P
Number of sites occupied	22	61		
Percent of sites occupied	55%	76%		
Date of first egg[a,b]	17 May	22 April	3.90 (81)	<0.001
Number fledged (brood)	1.8	3.0	−3.63 (81)	<0.001
Number fledged (season)	2.5	4.8	−3.26 (81)	0.002
Number of nesting attempts[b]	1.3	1.6	−1.71 (81)	0.086

[a] Analyzed as Julian date. Only first nesting attempts were used.
[b] Analyzed using Wilcoxon rank sum test.

Therefore, it is unlikely that a larger sample size would have led to a significant difference in bib sizes between males at SBNS's and DBNS's.

I also found no other morphological differences between males in DBNS's as compared to those in SBNS's (Table 2). The power of these tests also was low ($\text{power}_{d=0.2} = 0.11$; $\text{power}_{d=0.8} = 0.54$). However, for all traits except bill length, the differences between SBNS males and DBNS males was quite small, making it unlikely that significant differences would have been found with larger sample sizes. For bill length, a larger sample size might have indicated significant differences between males at SBNS's and those at DBNS's.

More young fledged during the season from DBNS's than SBNS's in 1992 but not in 1991 (Table 3). The increased reproductive success of pairs in DBNS's was due to an increased number of nesting attempts by DBNS pairs in 1992 and not to an increase in the number of young fledged per brood (Table 3). Data from 1991 also showed that pairs in DBNS's had greater reproductive success, and a larger sample size may have indicated significant differences in 1991 as well.

TABLE 2

DIFFERENCES IN MALE MORPHOLOGY BETWEEN MALES IN SBNS'S AND THOSE IN DBNS'S (1992 ONLY)

Variable	SBNS (N)	DBNS (N)	t (df)	P
Bib area (mm^2)	378.8 (8)	396.6 (7)	0.24 (13)	0.408
Wing chord (mm)	77.8 (12)	76.9 (9)	−1.02 (19)	0.159
Tarsus length (mm)	17.7 (12)	17.8 (9)	0.51 (19)	0.309
Bill depth (mm)	8.0 (12)	8.0 (9)	0.03 (19)	0.487
Bill width (mm)	7.4 (12)	7.4 (9)	−0.23 (19)	0.412
Bill length (mm)	9.8 (12)	10.4 (9)	1.70 (19)	0.077

TABLE 3

DIFFERENCES IN REPRODUCTIVE SUCCESS BETWEEN SBNS'S AND DBNS'S (1991: $power_{d=0.2} = 0.11$, $power_{d=0.8} = 0.54$; 1992: $power_{d=0.2} = 0.19$, $power_{d=0.8} = 0.93$)

Variable	SBNS	DBNS	z or t (df)	P
1991				
Number of sites occupied	8	14		
Percent of sites occupied	40	70		
Date of first egg[a,b]	12 May	19 May	−0.78 (20)	0.217
Number fledged (brood)	1.4	2.0	1.21 (20)	0.120
Number fledged (season)	1.6	2.9	1.43 (20)	0.085
Number of nesting attempts[b]	1.1	1.4	−0.89 (20)	0.188
1992				
Number of sites occupied	32	29		
Percent of sites occupied	80	73		
Date of first egg[a,b]	24 April	20 April	−1.23 (59)	0.109
Number fledged (brood)	2.9	3.1	0.45 (50)	0.328
Number fledged (season)	3.9	5.7	2.37 (59)	0.011
Number of nesting attempts[b]	1.3	1.8	2.64 (50)	0.004

[a] Analyzed as Julian date. Only first nesting attempts were used.
[b] Analyzed using Wilcoxon rank sum test.

Males occupying DBNS's did not obtain mates and begin reproducing prior to pairs at SBNS's (Table 3), contrary to what would be expected if the sparrows considered DBNS's superior to SBNS's. Significantly more DBNS's than SBNS's were occupied in 1991 (Fisher's Exact Test, N = 39, $P = 0.036$) but not in 1992 when sample sizes were larger (N = 80, $P = 0.378$). If DBNS's are more likely than SBNS's to be occupied, the trend is either weak or variable among years. Unoccupied DBNS's were always available in both years, indicating that at least some males chose to nest in SBNS's instead of DBNS's.

Pairs nesting in SBNS's could obtain clean nest boxes for renesting by moving to another nest site. Seven (of 11) SBNS pairs switched to another nest site before renesting. Although DBNS pairs had more nesting attempts than did SBNS pairs (Table 3), no DBNS pairs switched nest sites between nesting attempts. Therefore, while DBNS's were not consistently preferred, pairs in SBNS's often switched to new nest sites to renest, while pairs in DBNS's switched to the other nest box within the same nest site. The time between nesting attempts was the same for pairs which remained in a nest site and those which switched nest sites ($t = 1.12$, df = 38, $P = 0.271$), suggesting that there was little cost, as measured by delayed renesting, when pairs switched to a new nest site.

If switching nest boxes between nesting attempts is advantageous, one

would expect it to occur between most nesting attempts. Unused nest sites were always available on the study site, making such a strategy feasible. However, many pairs renested in the same nest box. In SBNS's, four of 11 pairs which renested did so in the original box. One SBNS pair nested successfully three times in the same box. Even in DBNS's, where a second nest box was already available on the nest site, a similar proportion (5 of 12 pairs) nested twice in the same box. Six DBNS pairs nested three times, and one of those pairs used only one of the two boxes in the nest site. Therefore, switching boxes between nesting attempts was neither a universal strategy nor necessary for successful reproduction.

DISCUSSION

Cavity nest sites are rare in many habitats (Martin 1993, Newton 1994), so cavities are an important resource for cavity nesting species unable to excavate their own cavity. If cavity nests are a scarce resource, (1) territories which contain multiple cavities may be preferred to territories with only a single cavity, (2) dominant or high quality males should be more likely to occupy territories with multiple cavities than will subordinate or low quality males, and (3) females should prefer to nest with males holding territories with multiple cavities.

In Europe, male House Sparrows with large bibs are dominant (Møller 1987a, b) and are more likely to obtain nest sites with multiple cavities (Møller 1988). In addition, male House Sparrows with experimentally enlarged bibs occupied more nest boxes than did control males (Veiga 1993). Contrary to those results, I did not find that males with large bibs were more likely to occupy nest sites with two boxes. Large-bibbed males fledged significantly more young during the breeding season than did small-bibbed males (Kimball 1995), suggesting that bib size does reflect at least some aspects of male quality in this population. There were also no other morphological differences between males in DBNS's and those in SBNS's. Although bib size was measured differently in all three studies, variance in bib sizes is large and it is unlikely that small differences in measurement technique would account for the different results.

In this study, I stacked nest boxes to create DBNS's which were likely to be defended by only one male. Veiga (1993) studied nest boxes placed 0.4–2.0 m apart, while Møller (1988) assessed potential natural nest locations, which would have been randomly distributed in the nesting site. The difference in nest dispersion between my study and those of Møller (1988) and Veiga (1993) may have affected the results. For example, separate nest boxes within a site might allow males to mate polygynously. About 10% of the males studied by Veiga were polygynous (Veiga 1990, 1992), while I only observed one polygynous male in two years (in this

case the nests sites were in separate trees). Veiga (1992) experimentally decreased the distance between boxes, to about 15 cm, and did not find that polygyny increased. This suggests that closely spaced boxes do not promote polygyny in House Sparrows, though polygyny may occur at sites with more distantly placed nest boxes. Therefore, the close placement of boxes in this study may have prevented males from attracting additional mates, and hence DBNS's were not preferred. Alternatively, a physical separation between multiple nests within a nest site may limit transmission of ectoparasites between nests, while nest boxes in physical contact may provide no such benefit.

Differences between the results I obtained and those of Møller (1988) and Veiga (1993) may be due to behavioral and ecological differences among populations. House Sparrow behavior is plastic, and other behavioral differences have been observed among different populations. For example, female choice for bib size has been demonstrated in Denmark (Møller 1988), but females do not prefer large-bibbed males in New Mexico, USA (Kimball 1996), and may not in Spain as well (Veiga and Puerta 1996).

Pairs in DBNS's had greater reproductive success in both 1991 and 1992, although results were only significant in 1992 when sample sizes were larger. These pairs gained a reproductive advantage because they were more likely to have multiple nesting attempts than were pairs in SBNS's. A clean nest box, which would have been readily available in DBNS's, may have increased the likelihood that a pair would renest. Supporting this idea, the majority of SBNS pairs which renested did so by switching to a new nest site. House Sparrows in other populations have also been observed to switch nest boxes between nesting attempts (Naik and Mistry 1980), indicating that it may be a common, although not necessary, occurrence.

In spite of the greater reproductive success of pairs in DBNS's, I could not detect a strong preference for DBNS's. DBNS's were not occupied prior to, or more commonly, than SBNS's. A preference for territories with two nest boxes has been demonstrated in Eastern Bluebirds (Meek and Robertson 1994, Plissner and Gowaty 1995). Eastern Bluebirds are obligate cavity nesters, whereas House Sparrows can nest successfully in non-cavity nests. Therefore nest boxes may be a more valuable commodity for Eastern Bluebirds than for House Sparrows. Other characteristics of the nest site, such as foliage structure, levels of human disturbance, or proximity to a food source may be more important for House Sparrows than number of nest boxes, which may not be true of species such as the Eastern Bluebird. In addition, unoccupied nest-box sites, as well as sites capable of supporting natural nests were always available, switching to a

new nest site may have involved relatively little cost, particularly when compared to the advantages some of the SBNS's may have offered.

There were several differences between 1991 and 1992. In 1991, when the boxes were new to the study site, seasonal reproductive success was lower and the breeding season began later relative to what I observed in 1992. These differences may indicate that the nest boxes were primarily occupied by younger birds in 1991 (Saether 1990), a phenomenon which may occur in House Sparrows (Lowther 1983). Therefore, the large proportion of DBNS's occupied in 1991 could indicate that DBNS's were easier for the inexperienced breeders to locate. The results from 1992, which included both young and old breeders, may therefore be more representative of typical House Sparrow populations in New Mexico.

I could find no morphological differences between males occupying DBNS's and those occupying SBNS's, suggesting that there are ecological and behavioral differences between this population and those in Europe (Møller 1988, Veiga 1993). DBNS's were not occupied prior to SBNS's, indicating that these nest sites may not have been preferred. Although DBNS's did not appear to be preferred, pairs in DBNS's had greater seasonal reproductive success, as pairs in these nest sites were more likely to renest. This paper emphasizes the need to study multiple populations to understand the constancy or plasticity of behavioral and ecological parameters.

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LIFE HISTORY OF THE ENDANGERED CAPE SABLE SEASIDE SPARROW

JULIE L. LOCKWOOD,[1] KATHERINE H. FENN,[2] JOHN L. CURNUTT,[1] DEBORAH ROSENTHAL,[3] KARLA L. BALENT,[1] AND AUDREY L. MAYER[1]

ABSTRACT.—Cape Sable Seaside Sparrows (*Ammodramus maritimus mirabilis*) breeding within eastern Everglades National Park were philopatric and moved only short distances between clutches. Incubation required 12 days, nestlings fledged at 9.2 days, and fledgling care ranged from eight to 20 days. The total nest cycle encompassed 34–44 days. Nestlings were fed spiders and insects, primarily Orthoptera, Lepidoptera, and Odonata. Diet varied between years and study sites. With the onset of summer rains, predation rate increased, and nest success decreased. Breeding activity diminished throughout June, coinciding with rising water in nest areas. Our results indicated that the lack of breeding habitat and the onset of summer flooding limit the breeding potential of Cape Sable Seaside Sparrows.
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In 1967, the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), was classified as endangered (32 Federal Register 4001, 1967). Since 1992, its population has declined by more than 50% (Pimm et al. 1996). Its secretive habits and the general inaccessibility of its preferred habitat have long discouraged a comprehensive study of its breeding cycle and diet. Here, we describe a two-year investigation of the biology of the species within eastern Everglades National Park. In particular, we provide information on nestling diet, nest cycle duration, nest success, and non-breeding activity. From these data, an accurate population model will be developed as an essential step in updating and implementing a recovery management scheme.

Howell (1919) discovered the Cape Sable Seaside Sparrow in the sparse salt marsh prairies of Cape Sable. Ignorance of the south Florida interior led to the assumption that the sparrow's entire range was in the Cape Sable area (Howell 1932). The September 1935 hurricane severely altered the landscape of Cape Sable causing the sparrow to disappear along with the prairies it inhabited (Pimm et al. 1996). Subsequent sightings of *A. m. mirabilis* were sporadic and unreliable until L. A. Stimson's search in 1955. Surprisingly, he identified several 'colonies' within freshwater marshes of the everglades (Stimson 1956). These sightings comprised the only known range of *A. m. mirabilis* until extensive surveys in 1981.

[1] Dept. of Ecology and Evolutionary Biology, Univ. of Tennessee, Knoxville, Tennessee 37996.
[2] South Florida Natural Resource Center, Everglades National Park, 40001 State Road 9336, Homestead, Florida 33034.
[3] 340 SE Lilly Avenue, Corvallis, Oregon 97333.

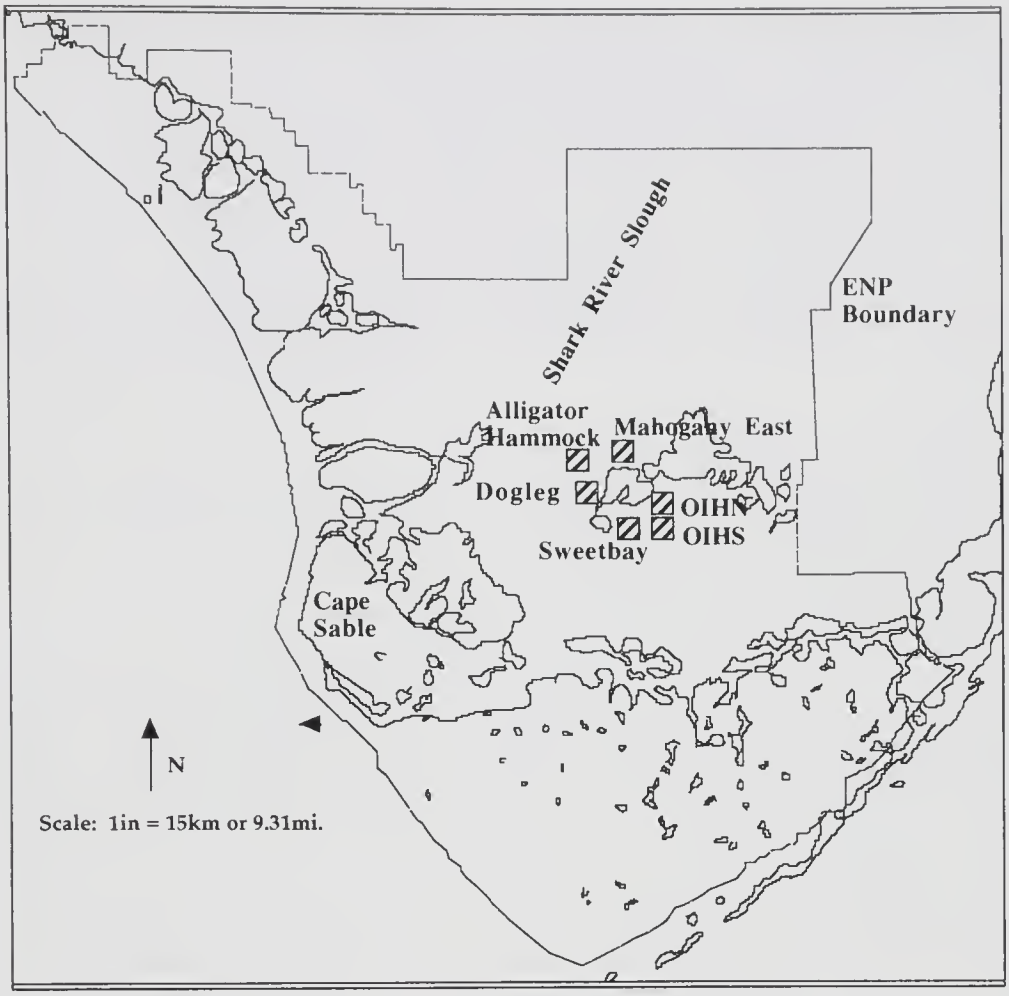

FIG. 1. All study sites were located within eastern Everglades National Park. Each is incorporated within a sub-population of the Cape Sable Seaside Sparrow, southeast of Shark River Slough.

The 1981 surveys indicated that Cape Sable Seaside Sparrows prefer short-hydroperiod freshwater prairies (Bass and Kushlan 1982, Kushlan and Bass 1983). Subsequent, breeding surveys defined two core areas that accounted for over 70% of all individuals (Pimm et al. 1996). One lies east, and the other lies west, of Shark River Slough (Fig. 1). Five areas of lower density and intermittent occupancy adjoin these locations to the east. Since 1993, the western population has declined sharply, while the eastern core population has remained nearly constant (Pimm et al. 1996).

STUDY AREA AND METHODS

We established six study sites (30–60 ha) east of Shark River Slough (Fig. 1). Water inundates all sites from July to December but recedes through most of the sparrows' breeding season (March through June). Muhly grass (*Muhlenbergia filipes*) and sawgrass (*Clad-*

ium jamaicense) dominate the vegetation. Frequent fires and a characteristic hydroperiod maintain the vegetative structure (Kushlan et al. 1982).

We made systematic nest searches and behavioral observations from late March through mid-August in 1995 and from early March through the end of July in 1996. Study area visits averaged one per week. We also made opportunistic observations from August 1995 until February 1996 within the Dogleg and Alligator Hammock sites (Fig. 1). We recorded the location, time, behavior, and all intraspecific interactions of individuals within each study area. We marked nests and monitored them until fledging or failure. During brief visits on alternate days, we recorded numbers of eggs hatching and fledging dates, and predation events. Daily, we observed what prey items were brought to the young, how often, and by which parent. We recorded the depth of surface water once per week at fixed stations within our study areas.

Observations of morning and late afternoon feedings averaged five hours per nest each week. We photographed adult sparrows holding prey items within 5–10 m of the nest. Comparing these photographs with observer notes corroborated identification of prey. We were unable to classify 25% of the prey items. Most unidentifiable prey items we estimated were less than half the sparrow beak length.

We sampled the insect communities in our plots using standard sweep-net protocols (see Pimm et al. 1995 for description of methods). To measure this population's relative use of prey orders, we compared prey available (sweep net samples) to prey taken (feeding observations) using the formula: Relative use = (% taken − % available/% available). We divided relative use data into three periods: 25 March–10 April, 11 April–25 April, 26 April–10 May 1996. By dividing the number of prey items taken in one period by the total number of prey items taken for all periods, we calculated the percent taken. We used the same formula to calculate the percent available. We interpreted relative use as: under-represented (<zero), neutral (≈zero), or over-represented (>zero).

Using Chi-square contingency tables, we compared proportional representation among prey taxa between years (1995, 1996) and sites (Dogleg, OIHN, and OIHS). Our analyses included only those orders that incorporated more than 5% of the total number of individuals in either sweep net or feeding samples. We did not include two sites for which prey observations were minimal.

Schaub et al. (1992) provided the method of estimating predation rate that we employed. This method calculates predation rate by dividing the number of apparent predation events by the total number of days that nests contained eggs or young. We assumed predation when clutches disappeared between observations or when we found direct evidence such as broken eggshells or destroyed nests. The rate calculation gives equal weight to all methods of predation detection.

RESULTS

Breeding season duration.—In 1995, the first nest (found 18 April) held nestlings 5–6 days old. In 1996, we found a nest in which the first egg was laid on 27 March. We estimated that nest building began around mid-March. Werner (1975) observed flightless fledglings as early as 2 April indicating that these nests were built in late February. Thus, it appears that the onset of nesting varies only by a few weeks annually.

Cessation time may vary by as much as a month or more, however. Werner (1975) reported observing eggs as late as 7 July, 1974 and nestlings as late as 26 July, 1974. The next year (1975) he reported that

nesting ceased in early July concurrent with the onset of summer rains. In our study, the latest nesting activity occurred in mid-May 1995 and late June 1996, also concurrent with the onset of summer flooding.

Nest success.—Searches during the 1995 and 1996 breeding seasons yielded 24 nests. Four of five 1995 nests and 13 of 19 1996 nests were first clutches. We positively identified four second clutch attempts in 1996 and none in 1995. One nest in 1995 and two in 1996 coincided with known second clutches. A nest found with eggs in late June 1996 was a positively identified third clutch.

Using the Mayfield method (Mayfield 1975), we calculated a hatching success rate of 88% (N = 14, 28 young from 32 eggs)—a rate common for Seaside Sparrows (Post and Greenlaw 1994). This population laid an average of 3.2 eggs per nest (N = 14, range = 2–4, mode = 3,4). This is consistent with the clutches found by Werner (1975) at Taylor Slough but somewhat smaller than northern populations of Seaside Sparrows (Post et al. 1983, Post and Greenlaw 1994). Each nest, on average, contained three nestlings (range, 2–4, N = 14).

Werner (1975) calculated a crude nest success rate (i.e., the number of fledglings resulting from a known number of eggs) of 62% (N = 16). In our study, 15 young fledged from 26 first-clutch eggs. None of eight second-clutch eggs hatched. The sole third clutch of two eggs was abandoned. Overall, we found 36 eggs from which 15 young fledged (N = 14). This gives a crude success rate of 42% which is below that reported by Werner (1975).

Breaking down nest success using the methods of Mayfield (1975) and Johnson (1979) more accurately reflected annual productivity. The probability of success for a Cape Sable Seaside Sparrow nest through 12 days of incubation (see below) was 0.61 (SE = 0.02, N = 13, 75 nest-days with 3 losses). The probability of success for a nest through the nine days of nestling care was 0.75 (SE = 0.02, N = 18, 125 nest-days, 4 losses). Multiplying these with the 0.88 probability of hatching gave the probability of an egg successfully producing a fledgling equal to 0.40. Thus, only 40% of all eggs laid will contribute to the total population annually.

In 1996, water directly influenced the success of two nests. The first, found on 6 June with four eggs, hatched three young on 8 June. When water flooded the bottom of the nest on 12 June, all nestlings disappeared. The water level was 15 cm deep, a depth 1 cm above the bottom of the nest. The second nest, discovered on 20 June with two eggs, flooded two days later and incubation ceased. Here, the water level was 23 cm deep, again 1 cm above the bottom of the nest.

Predation accounted for 78% of all losses of young or eggs. In the first five weeks of the breeding season, a nest succumbed to predators on less

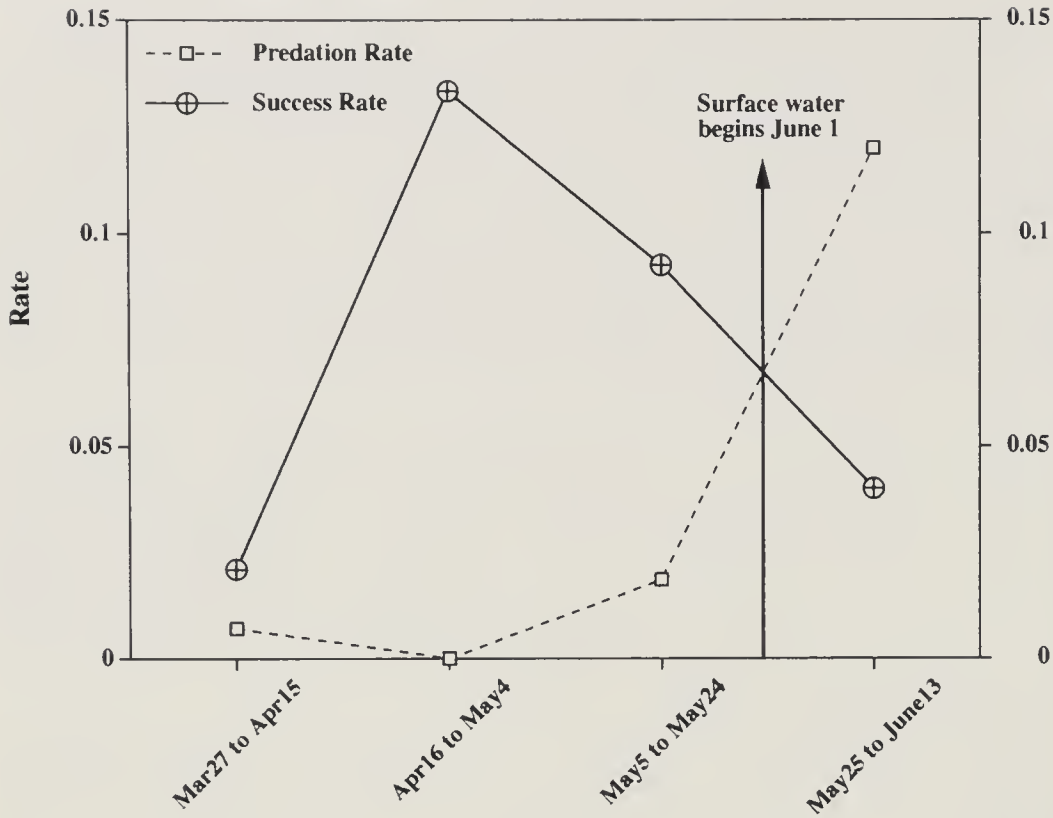

FIG. 2. Predation and success rate for 1996 nests. An increase in nest predation, a decrease in nest success, and the appearance of surface water coincided around June 1, 1996.

than 3% of all the days when eggs or nestlings were present (Fig. 2). Beginning in late May, this rate reached 13%. Thirteen nests were first clutches. Only two of the other six nests (i.e., second and third attempts) successfully fledged young.

The presence of surface water corresponded with the late season increase in predation rate. To show this, we calculated success rate in a way comparable to predation rate. We divided the number of hatching or fledging events by the number of days nests held young or eggs. The two rates intersect in early June. June 1 marked the beginning of consistent coverage of all study sites with surface water (Fig. 2).

Kushlan et al. (1982) suggested that rice rats (*Orzymus palustris*) and snakes principally threaten nests. Post (1981) indicated that rice rats, fish crows (*Corvus brachyrhynchos*) and raccoons (*Procyon lotor*) threatened Seaside Sparrow populations in northern Florida. As we have never directly observed any predation events, we cannot speculate on what advantages the presence of surface water may afford predators.

Phenology.—We followed one nest throughout egg laying and incubation. A complete nest found on 22 March did not contain its first egg

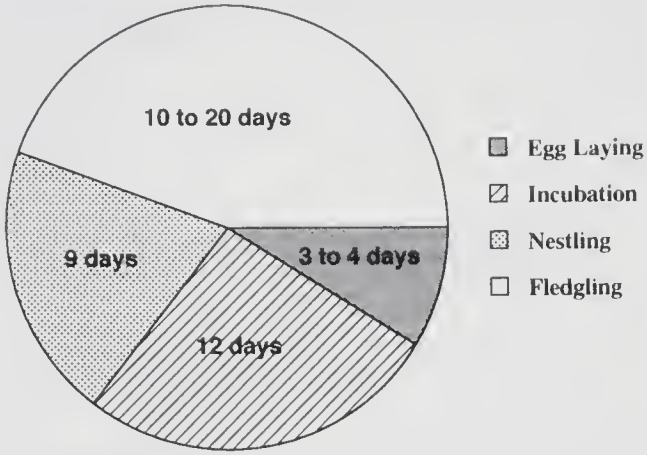

FIG. 3. Cape Sable Seaside Sparrow nest cycle duration encompasses, at the most, 44 days. Thirty-five of those days can be accounted for through previous observations. The remaining 14 are devoted to courtship, nest building, and other activities (e.g., fledgling care, independent feeding).

until 27 March. The female laid the second and last egg on 29 March. She then incubated the eggs for 12 days. This is the first direct observation of Cape Sable Seaside-Sparrow incubation length. An incubation period of 12 days is consistent with other populations of Seaside Sparrows (Post and Greenlaw 1994). It is unclear how common it is for *A. m. mirabilis* females to lay every other day. Post and Greenlaw (1994) indicated that most races of Seaside Sparrows lay one egg per day. Since the average number of eggs laid for this population is 3.2, the number of days devoted to egg laying is likely three or four days.

Nestlings fledged after an average of 9.2 days in the nest (N = 15). For two to three days, they remained sheltered under vegetation 5–10 m from the nest. Observations of fledgling–adult interactions were sporadic. We observed adults feeding juveniles eight days after fledging, and Werner (1975) observed adults feeding juveniles up to 20 days after fledging.

Totaling these numbers, we estimated the nest cycle of *A. m. mirabilis* to be 34 to 44 days. This number varies according to the number of eggs laid and the length of post-fledging care (Fig. 3). Since nesting appears to began in mid-March, a pair that successfully triple brooded (at least 44 days times 3) would maintain breeding activity into early August. This schedule falls within the observations of Werner (1975) and those reported in Post and Greenlaw (1994).

Nestling diet.—Six orders of Insecta and one order of Araneida comprised the observed nestling diet. Males brought food to nestlings in 52% and females in 48% of all visits (N = 251). Feedings occurred approximately every 16 minutes (N = 1242) and adults commonly carried more than one insect per trip (average = 1.35; SD = 0.56, N = 260). Since

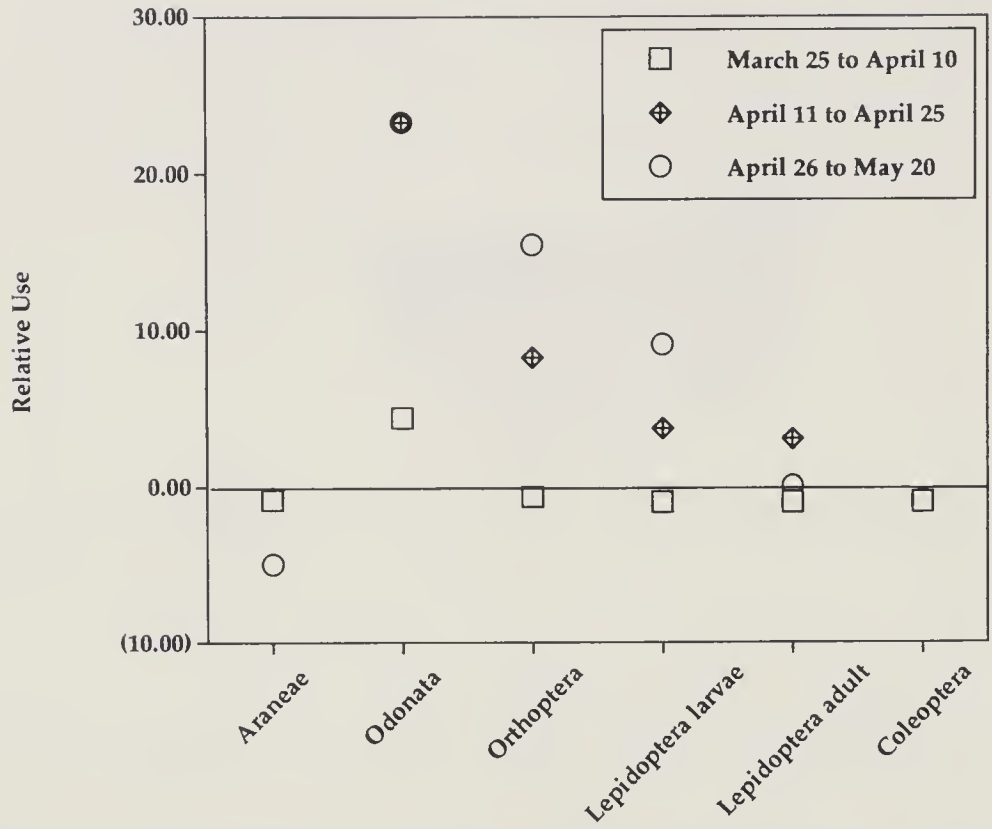

FIG. 4. Relative use of prey items in nestling diet. Availability was based on sweep net samples. Prey use was based on observations made on 1996 nests.

adults often carried only the abdomens of Odonata and Orthoptera, we suspected that they either ate or discarded all other parts before arriving at the nest. Post and Greenlaw (1985) reported that adults of other races presented macerated or mucous-bound food items to nestlings.

Nestling diet included Lepidoptera, Orthoptera, and Odonata to a greater extent than expected by their availability in 1996 (Fig. 4). Conversely, it rarely included Coleoptera and Araneae, despite these orders comprising 88% of the available food items. Relative use of prey items changed over the course of the breeding season. Early in the season (25 March to 10 April), sparrows used only Odonata more frequently than would be expected based on their availability. While disproportionate use of this group persisted to the end of the season, by mid-season (11 April to 25 April) parents also began feeding nestlings Orthoptera and adult Lepidoptera. At the end of the season (26 April to 20 May) the parents switched from Lepidoptera adults to larvae but, continued their disproportionate use of Orthoptera and Odonata.

Nestling diet changed between years ($\chi^2 = 59.1$, df = 4, $P \ll 0.001$, Fig. 5). In 1995, Odonata represented nearly 30% of the nestling diet. In 1996, this number dropped to under 10%. Conversely, Orthoptera ac-

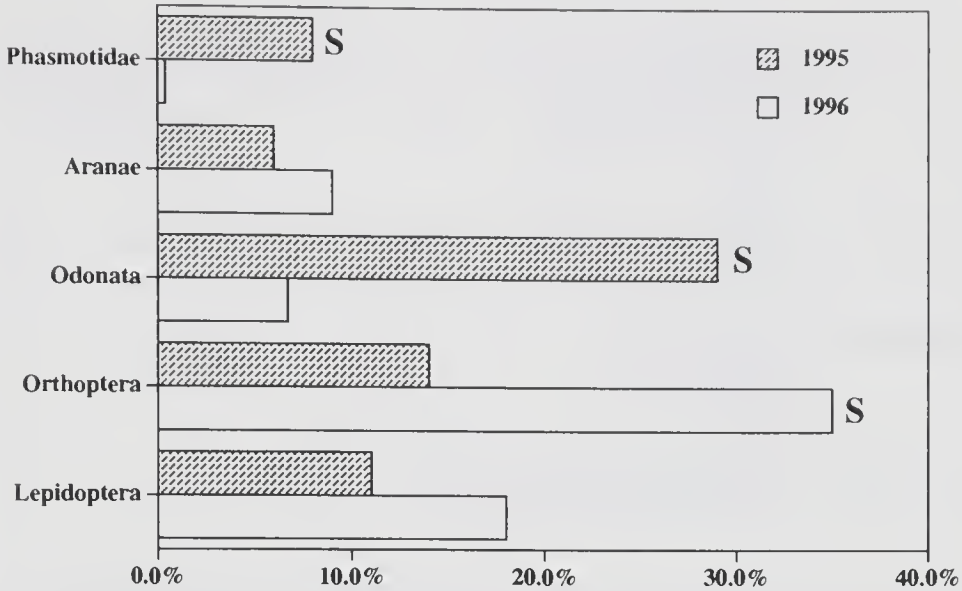

FIG. 5. Composition of nestling diet by insect order. Data collected from first clutch nests in 1995 and 1996. S = significant difference between years.

counted for only 15% of nestling diet in 1995, but exceeded 35% in 1996. Phasmotidae were absent from nestling diets in 1996 but comprised nearly 10% of it in 1995.

Nestling diet data from 1996 also showed differences among sites ($\chi^2 = 31.5$, df = 8, $P < 0.001$). Odonata were absent from nestling diets at OIHN despite their presence at all other sites (Fig. 6). Lepidoptera were absent from Dogleg, but common at OIHN. Orthoptera had equal representation at each site, as did an unidentified (but distinct) species.

Seasonal and yearly movements.—Male Cape Sable Seaside Sparrows exhibited a high degree of philopatry—a common trait in all Seaside Sparrow races (Post and Greenlaw 1994). In 1996, three males nested an average of 40 meters away from their 1995 nests. Second clutch nests ranged eight to 95 m from the site of the first clutch nest. Sparrows never reused nests. After nest destruction, we observed males attending a nest within the same territory. Since very few females have been banded, we do not know if the re-nest attempts by these males included the same females as well.

Observations of where *A. m. mirabilis* spends the wet-season (post-breeding) are less detailed. Werner (1975) suggested that rising surface water ended the nesting season but provided no further information. Breeding behavior ceased in two of our study areas when surface water reached the average height of nests above the ground (14 cm). Adults remained within established territories and defended juveniles until surface water appeared. Afterwards, observations of females became rare, and some males disappeared. Those males that remained moved into va-

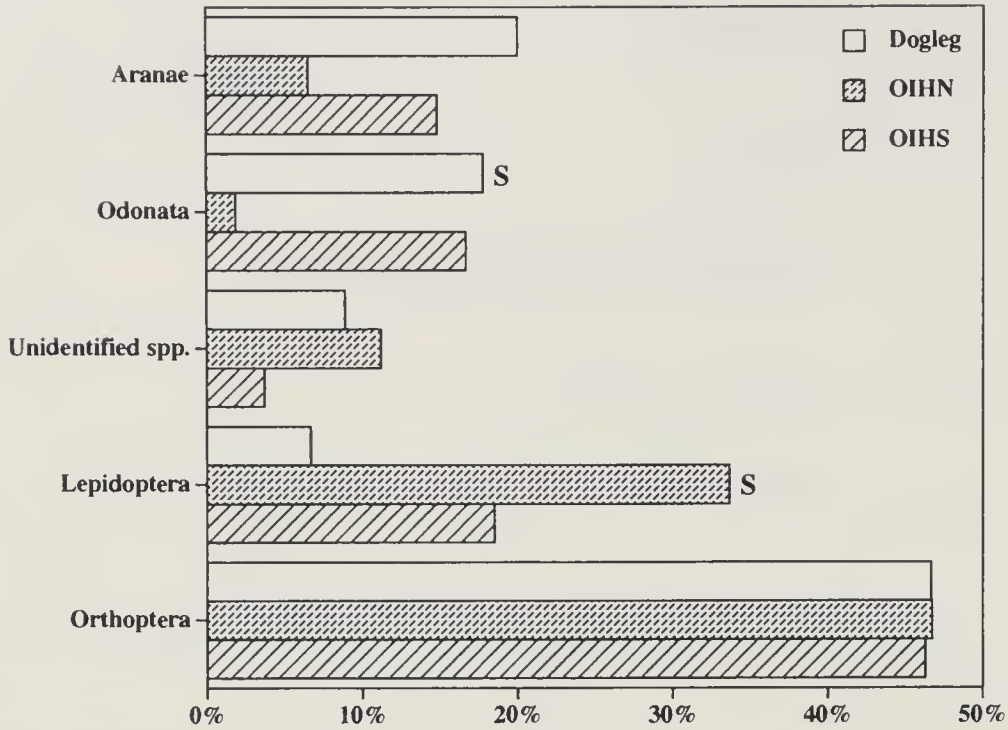

FIG. 6. Between-site differences in composition of nestling diet. S = significant differences between sites.

cant neighboring territories or into taller, denser vegetation. They continued to sing and defend juveniles. Although juveniles tended to associate with a particular male, we observed a group of seven with two banded males outside any nesting territory. Water levels peaked at 18 cm in late June, with a subsequent dry-down occurring in mid-July (down to 4 cm). Breeding activity however, never resumed. We observed sparrows around tree islands and sawgrass sways from late June into July (B. Moody and T. Brooks pers. comm.). Males sang sporadically in open prairies throughout the remainder of the winter.

DISCUSSION

The Cape Sable Seaside Sparrow is a dietary generalist. We detected significant differences in nestling diet between years and sites. In addition, sparrows shifted the importance of prey items in their diet with their availability. This reflects the patchy distribution typical of insects and the opportunistic nature of sparrow foraging (Post and Greenlaw 1994).

Cape Sable Seaside Sparrows rely on Orthoptera and Lepidoptera much like all other races (Post et al. 1983, Merriam 1983). The absence of Diptera and other mud-dwelling insects from the nestling diet is consistent with Seaside Sparrow populations studied in northern Florida (Post et al. 1983). This behavior contrasts that of sparrows inhabiting salt marshes in

the northern parts of the species' range (Merriam 1983). Southern races, including *A. m. mirabilis*, depend less on open mud flats (Post and Greenlaw 1994, Quay et al. 1983). There are few, if any, expansive mud flats within our study areas. Cape Sable Seaside Sparrows appear unique among the Seaside Sparrow races in their use of Odonata. This is not surprising, since this is the only race inhabiting freshwater marshes.

Breeding consistently begins in March and potentially continues into early August. The sparrow may fledge three broods given suitable conditions. Since *A. m. mirabilis* is a breeding habitat specialist (Pimm et al. 1996), consistently available habitat will increase sparrow breeding potential.

Two factors, each working at different temporal scales, limit the sparrow's reproductive potential, however. The first, which we do not address here, is the dynamic nature of sparrow breeding habitat. Long-term hydrologic conditions and fire may rapidly change vegetative composition of marl prairies (Pimm et al. 1996). A philopatric male may find his territory unsuitable for breeding from one year to the next. Second, the onset of summer rains limits the breeding season, as the flooding of two nests demonstrates. The beginning of the wet season varies. Thus, with a series of 'good years' (those with delayed summer rains), sparrow populations may increase considerably. Conversely, with a series of 'bad years' (those in which summer rains begin early) Cape Sable Seaside Sparrow populations may decrease substantially.

We still lack a complete knowledge of the sparrows' wet season dispersal and habitat requirements. In other races, individuals moved to sheltered areas consisting of tall smooth cordgrass (*Spartina alterniflora*) after the breeding season (Post and Greenlaw 1994). The higher concentrations of insects (Post et al. 1983) and seeds in cordgrass presumably attracted individuals (Post and Greenlaw 1994). The same may be true for sawgrass sways in everglades freshwater prairies. In addition, the unique south Florida climate may or may not produce novel wet season (or over-wintering) adaptations.

The next step in formulating a reasonable recovery strategy is linking the known aspects of sparrow breeding biology to this temporally variable environment. Population models of the Cape Sable Seaside Sparrow, even spatially explicit ones, must incorporate stochastic environmental factors. When this information is available, results from population models will be applicable to management schemes.

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SHORT COMMUNICATIONS

Misdirected incubation in American Kestrels: a case of competition for nest sites?—Reports of birds exhibiting unusual incubation behaviors are perhaps not surprising, given the wide variety of physical properties that can elicit incubation responses in birds (see Baerends and Drent 1982). Birds that normally are solitary nesters occasionally have been documented sharing the same nest site (Terres 1982, Fournier and Hines 1996). Parent birds have also inadvertently hatched or raised offspring of a different species (Tlusty and Hamerstrom 1992, Breen and Parrish 1996). When nest sharing or cases of parent birds raising non-conspecific offspring occur, it frequently is assumed to be the result of competition for nest sites (e.g., Simpkin and Gubanich 1991). Here we report on the multiple use of a nest box. Two pairs of American Kestrels (*Falco sparverius*) and a Bufflehead (*Bucephala albeola*) occupied this nest box during the season, suggesting intense competition for this particular site, despite the fact that natural cavities do not appear to be limiting on our study area (Bortolotti 1994; pers. obs.), and that there were several nest boxes in the vicinity that were unoccupied. Use of this nest box by kestrels and Buffleheads, both secondary cavity nesters, resulted in an unusual event where by a pair of kestrels successfully incubated and hatched a Bufflehead egg in addition to their own clutch.

Methods.—We have studied American Kestrels in the boreal forest of north central Saskatchewan (55°N, 106°W) in the vicinity of Besnard Lake since 1988. Kestrels arrived on our study area in mid- to late April and began laying eggs in mid-May. Nest boxes contained a few centimeters of wood shavings, and we visited boxes in late April to evict red squirrels (*Tamiasciurus hudsonicus*) that frequently occupy nest boxes during the winter. We again checked nest boxes approximately every three to five days between mid-May and mid-June to determine laying date. Further details of our general methods can be found elsewhere (Bortolotti 1994, Dawson and Bortolotti 1997).

Observations.—On 27 April, 1996, a red squirrel was found in a nest box along with a grass nest. Both the squirrel and its nest were removed. Two days later, a squirrel and a grass nest were again removed from the nest box. The next visit occurred on 14 May and, although no kestrels were seen in the area, the presence of a scrape in the wood shavings lining the nest box suggested that the territory was occupied by kestrels. We levelled the scrape in the wood shavings before leaving. Upon approaching the nest box five days later (19 May), a color-banded female kestrel flushed from the nest, although we did not ascertain her identity. A scrape with no eggs was found during that visit.

During the next visit on 24 May, we found one large egg in the box that was undoubtedly laid by a duck. No ducks or kestrels were sighted in the area. The duck egg was olive-buff in color and measured 53.5mm by 36.6mm, which suggests it was layed by a Bufflehead (see Bellrose 1976). Expecting to find an incubating female Bufflehead when we returned to the nest on 15 June, we were surprised by the presence of an unbanded female kestrel in an incubating posture. Upon lifting the kestrel from the eggs to band her, we noted that she was not only incubating four of her own eggs but also the duck egg. RDD estimated by candling (Weller 1956) that the duck egg was in its 7th to 9th day of incubation. The female kestrel was placed back on the eggs and was again incubating all five eggs during a visit on 25 June.

On 1 July, the male kestrel was captured while incubating the four kestrel eggs and a single duck egg. This male was previously banded and was at least three years old. He had bred successfully in nearby nest boxes during 1994 and 1995. On this visit, the duck egg

was estimated to be in its 22nd day of incubation. On 4 July, the female kestrel was present and three of four kestrel eggs had star cracks. The duck egg had 25 days of incubation. Two kestrel chicks had hatched by 6 July and were being brooded by the female kestrel. On 8 July, the duck egg had reached the pipping stage, and the remaining two kestrel eggs had star cracks but appeared to be dead. A visit on 9 July revealed that the duckling was nearly emerged from its egg. On 10 July, the nest contained two kestrel chicks approximately five days old plus the day-old duckling. The duckling on this visit was highly mobile and repeatedly attempted to jump up towards the nest box hole. The duckling was not present in the nest box on 12 July, and we could find no evidence that it had been killed by the kestrels (i.e., no prey remains). Because of its highly mobile nature on the previous visit, we suspect that the duckling left the nest box on its own accord. The remaining two unhatched kestrel eggs were removed during this visit and found to contain fully developed embryos that died just prior to hatching. The remaining two kestrel chicks fledged normally several weeks later.

Discussion.—We find it remarkable that this pair of kestrels was able to incubate the duck egg and two kestrel eggs, as well as incubate two other kestrels eggs nearly to hatching. Using Hoyt's (1979) equation, we calculated the volume of the Bufflehead egg to be 36.5 cm^3, while the average egg volume of the four kestrel eggs in this nest was 12.7 cm^3. The total egg volume that the kestrels incubated in this nest was therefore 87.3 cm^3, the equivalent of nearly seven kestrel eggs. Kestrels potentially have difficulty incubating a normal clutch of five kestrel eggs, and clutches of six kestrel eggs, which are relatively rare, frequently experience partial hatching failure (Wiebe and Bortolotti 1993; unpubl. data).

Birds of prey have previously been documented incubating waterfowl eggs. However, these reports are of Black-headed Ducks (*Heteronetta atricapilla*), which are obligate brood parasites, laying eggs in Snail Kite (*Rostrhamus sociabilis*) and Chimango Caracara (*Milvago chimango*) nests (Weller 1968, Höhn 1975). The difference in egg sizes between those of Black-headed Ducks and kites or caracaras is not as pronounced as those we report here (see Weller 1968, Brown and Amadon 1989). We suspect that the female kestrel in this study could easily have moved the duck egg to one corner of the next box or chosen to lay her eggs away from the duck egg. In either case, incubation of the duck egg was not required. It may be that the presence of this abnormally large egg in the nest was a "supernormal stimulus" (Tinbergen 1951), resulting in the pair's showing tenacious incubation behavior and being relatively successful at applying sufficient heat to an unusually large volume of eggs.

We lack information on whether the first pair of kestrels was usurped by the Bufflehead and whether the Bufflehead was in turn displaced by the second pair of kestrels. Erskine (1964, 1971) reported that Buffleheads had displaced other species and are themselves occasionally displaced, usually by passerines. Regardless, these observations suggest that there is competition for nest sites in our study area. However, occupancy of our nest boxes by kestrels during 1996 was only 38% (N = 376 boxes), and natural cavities were extremely abundant (Bortolotti 1994; pers. obs.). In addition, two nest boxes adjacent to box #99 were unoccupied, with the closest only 400 m away. We suggest that rather than there being intense competition for all nest boxes (see also Bortolotti 1994), there was a desirable quality associated with this particular nest box.

The habitat where box #99 is located consists almost entirely of young jack pine (*Pinus banksiana*). We propose that, because of the relatively young age of the forest, there may be a paucity of natural cavities in this immediate area but not on the study area as a whole. Additional evidence for limited nest sites in this particular area is that this nest box as well as the one 400 m away were occupied by Boreal Owls (*Aegolius funereus*) in 1993, a species

that normally does not use nest boxes on our study area (Gerrard et al. 1996), presumably because of abundant natural cavities.

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Russell D. Dawson and Gary R. Bortolotti, *Dept. of Biology, Univ. of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, Canada, S7N 5E2.* *Received 31 Oct. 1996, accepted 20 April 1997.*

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Nest reuse by Western Kingbirds.—Nest reuse is apparently uncommon among passerine species that build open-canopy nests (Mountjoy and Robertson 1988, Petit and Petit 1988, Curson et al. 1996), but there are anecdotal reports for species such as the American Robin (*Turdus migratorius*), Prairie Warbler (*Dendroica discolor*), Eastern Kingbird (*Tyrannus tyrannus*), Cedar Waxwing (*Bombycilla cedrorum*), and Prothonotary Warbler (*Protonotaria citrea*) (Tyler 1949, Nolan 1978, Blancher and Robertson 1985, Mountjoy and Robertson 1988, Petit and Petit 1988). I am unaware, however, of any systematic studies of nest reuse for any canopy-nesting passerine species.

Western Kingbirds (*T. verticalis*), which are Neotropical migrants, commonly inhabit open and partially open areas with scattered trees (see Gamble and Bergin 1996). Pairs mate monogamously throughout the breeding season, normally raising a single brood. Western Kingbirds defend a nesting territory and build an open-canopy nest from grass, twigs, and other string-like materials. Females perform most, if not all, of the nest-building activity, while males stand guard. Western Kingbirds have reused nests of other species such as Northern Flickers (*Colaptes auratus*), Baltimore Orioles (*Icterus galbula*), and Bullock's Orioles (*I. bullockii*) (Quigley 1944, Pinkowski 1982, Kennedy 1915, Munro 1919, Bergin 1992). There is one historical record of Western Kingbirds reusing a conspecific nest; a new nest was built on top of the old (Hunter 1915).

The study sites were in the Lake Ogallala State Recreation Area adjacent to the Kingsley Dam of Lake MacConaughy in western Nebraska. The habitat was riparian woodland with interspersed grasses and forbs. Data on nest reuse were collected while studying the nesting ecology of Western Kingbirds from 1989–92. A nest found in a previously used nest site was considered "old" and was then visited at least every other day throughout the current breeding season to determine its fate: unused, reused-failed, and reused-successful.

Twenty-five out of 76 (33%) active Western Kingbird nests constructed from 1989 to 1991 survived to the next breeding season; of these, 18 had been successful the previous season. Of the surviving nests, 19 (76%) were reused by three different species (Table 1) including Mourning Doves (*Zenaida macroura*) (N = 8), Eastern Kingbirds (N = 1), and Western Kingbirds (N = 10). Of the nests reused by Western Kingbirds, six were successful (60%), two suffered wind damage (20%), one suffered nest predation (10%), and one was abandoned, compared to a success rate of 52%, wind damage of 15%, and nest predation of 33% for all other active Western Kingbirds nests from 1989 to 1992 (Bergin 1993). Seven of the nests reused by Western Kingbirds had previously been successful. Western Kingbirds were not banded, so individual recognition was not possible. It is possible, however, that some nests were reused by the same individuals that constructed them.

These observations illustrate the behavioral plasticity of Western Kingbirds which nest in many different structures, including trees, cacti, power poles, buildings, and windmill towers (Gamble and Bergin 1996). Some Western Kingbirds reuse old conspecific nests when available—often successfully. Even nests of other species are reused (Kennedy 1915, Quigley 1944, Bergin 1992). Some Western Kingbirds exhibit site fidelity after nesting successfully (Blancher and Robertson 1985, Gamble and Bergin 1996) and thus may be predisposed to reuse old nests.

Nest building is an energetically expensive activity because as many as 2500 trips may be required to build an adequate nest (Putnam 1949, Collias and Collias 1984). In addition, trips to acquire nest material potentially expose birds to an increased risk of predation (Lima and Dill 1990). These costs can be reduced considerably if old nests are reused, but the strategy of nest reuse has several drawbacks (Collias and Collias 1984, Mountjoy and Robertson 1988). First, old nests are more likely to carry diseases or ectoparasites. Second, old

TABLE 1
NEST REUSE BY WESTERN KINGBIRDS

Fate of nests constructed by Western Kingbirds	1989	1990	1991	1992	Total
Total number of active nests	22	27	27	20	96
No. surviving from previous breeding season	*	4	11	10	25
No. unused	*	1	3	3	7
No. reused	*	3	9	7	19
Western Kingbird	*	0	6	4	10
Eastern Kingbird	*	0	1	0	1
Mourning Dove	*	3	2	3	8
Fate of nests reused by Western Kingbirds					
Successful	*	0	4	2	6
Unsuccessful	*	0	2	2	4
Wind	*	0	1	1	2
Predation	*	0	0	1	1
Unknown	*	0	1	0	1

* Data unavailable.

nests are unpredictable resources that are unlikely to survive to the next breeding season. Third, the reuse of old nests increases the probability of nest failure due to prior structural damage. Researchers examining the trade-offs between the costs and benefits of nest reuse should consider an experimental approach (Rendall and Verbeek 1996a, b).

Nest reuse is rarely reported for canopy-nesting passerines (Curson et al. 1996). The reasons are unclear. Perhaps old nests are difficult for researchers to track. Nest reuse by Western Kingbirds was documented only after a systematic search-effort during a multi-year study. Perhaps nest reuse is truly rare for canopy-nesting passerines. Only long-term studies of many species will reveal its true prevalence.

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TIMOTHY M. BERGIN, *Dept. of Animal Ecology, Iowa State Univ., Ames, Iowa 50011.* *Received 13 Aug. 1996, accepted 20 April 1997.*

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Tawny Fish Owl activity pattern.—Fish owls, often regarded as nocturnal counterparts of the diurnal Osprey (*Pandion haliaetus*), fish eagles *Ichthyophaga* spp., and sea eagles (*Haliaeetus* spp.), consist of four species in the genus *Ketupa* from Asia and three species in the genus *Scotopelia* in Africa (Fogden 1973). Little is known about the natural history of the rare, seclusive Tawny Fish Owl (*Ketupa flavipes*) (Voous 1988). To date, no consensus has been reached regarding the circadian rhythm of the Tawny Fish Owl. Ali (1986), Severinghaus (1987), and Meyer De Schauensee (1984) described the owl as crepuscular and partially diurnal in habit. In Taiwan, Chang (1985) noted that Tawny Fish Owls were nocturnal, whereas Yeng (1985) reported them to be diurnal or crepuscular (Wang et al. 1991). These discrepancies are likely based on the results of scanty observations. In this paper, we examine the activity pattern of this species.

Methods.—We conducted field studies at Fusan, Nanshih Stream, 350 m in elevation, approximately 30 km south of Taipei, Taiwan. Vegetation consisted mostly of tropical rainforest formations dominated by *Ficus* and *Lauraceae* on the east and south banks of the stream (Taiwan Forestry Bureau 1995), whereas plantations, mostly of Makino Bamboo (*Phyllostachys makinoi*) and Japanese Fir (*Cryptomeria japonica*), farmland, and human

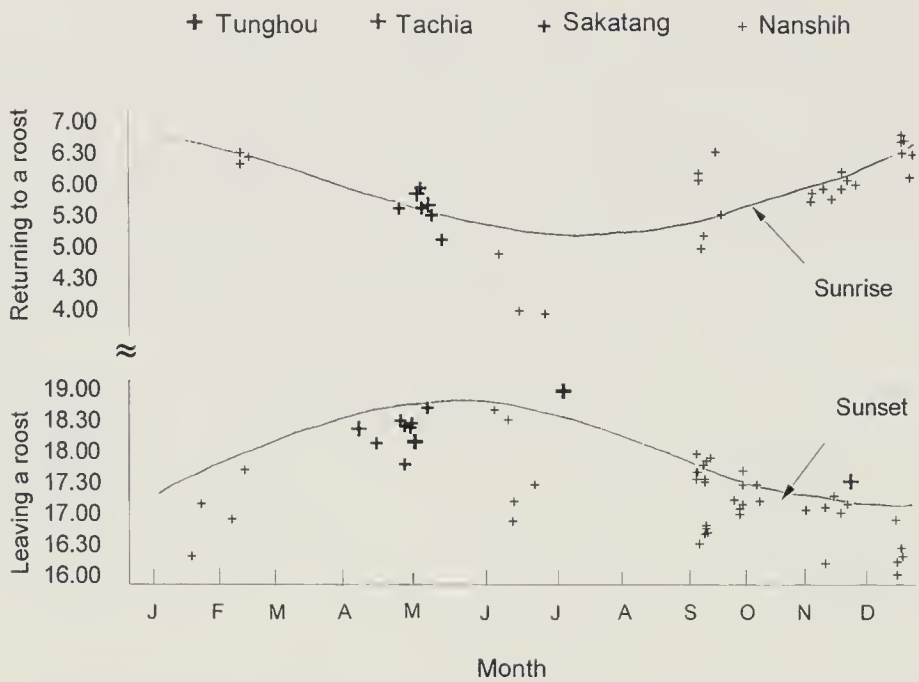

FIG. 1. Activity period of Tawny Fish Owls on the Nanshih, Tachia, Tunghou, and Sakatang streams, 1994–1996. Crosses indicate when activity began and ceased in relation to sunset and sunrise by stream location. Each point represents one record.

habitation occur mainly on the west bank. We recorded additional data with respect to the time when Tawny Fish Owls left and returned to their roosts at Tachia, Sakatang, and Tunghou streams.

From October 1994 through July 1996, we captured four Tawny Fish Owls using foot-snare traps on nighttime foraging perches or on pond banks of fish farms at the Nanshih Stream. Owls were leg-banded, and radio-tagged prior to release. Radio transmitters had activity sensors (MD-205; Telonics Inc., Mesa, Arizona), weighed 70–80 g (<4% of the owl's body mass, 2.1–2.6 kg) and had a lifespan of about two years. They were attached dorsally with a backpack harness of wire (1.5 mm in diameter) wrapped inside a tubular teflon ribbon. We recorded radio signals of the owls with a directional hand-held H-antenna with a TR-2 receiver (Telonics Inc., Mesa, Arizona).

To estimate the temporal activity pattern of the owls, we recorded radio signals of each owl for at least two 10-min periods each hour in one 24-h period approximately biweekly. The activity sensor of the transmitter generated two pulse rates on the basis of whether the bird was active (e.g., preening, walking, flying, and foraging) or inactive. It produced 37 pulses per minute (PPM) during owl inactivity and 54 PPM during owl activity. Over each hour period, two types of activities were recognized and measured: (1) all activity (sum of active pulses/[54 × 60]) × 100% and (2) moving activity (sum of active pulses with movement/[54 × 60]) × 100%. Owl movement could be detected from the fluctuations in radio signal strength, which we used as the index of foraging activity. Based on direct observation of a captive Tawny Fish Owl, non-movement activities such as head-turning (N = 93), body-turning (5), and preening (7) did not change the radio signal strength. We used the Mann-Whitney and Kruskal-Wallis test (Conover 1980) to compare between two or more independent sample populations, respectively.

Results and discussion.—Activity periods of Tawny Fish Owls coincided with diel pattern (Fig. 1). The time the owls went to their day roosts averaged 8.18 ± 31.59 min (range =

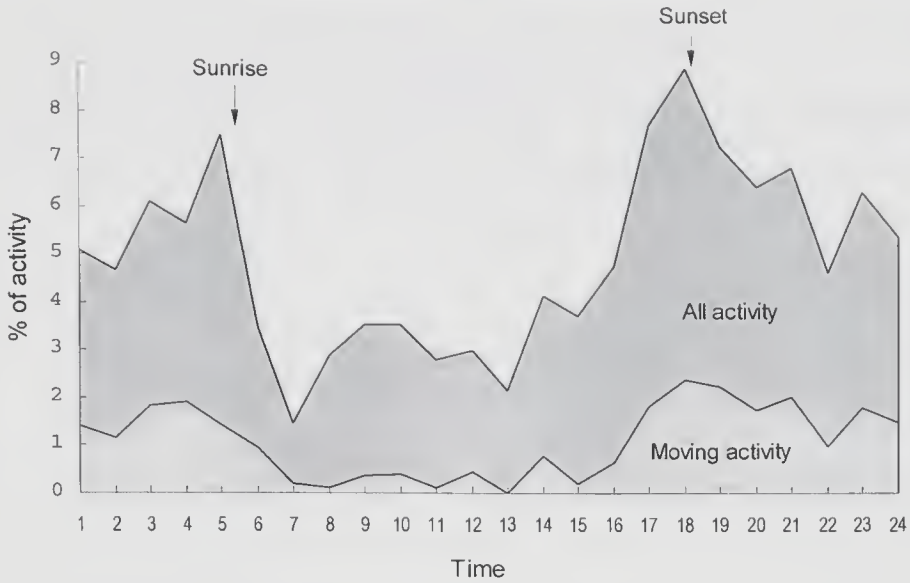

FIG. 2. Temporal variation in the percentages of all activity and movement of four radio-tagged Tawny Fish Owls at Nanshih Stream during 1993–1996.

−83 to 55 min, N = 34) prior to sunrise, and they left their roosts for foraging about 5.77 ± 35.59 min (range = −105 to 35 min, N = 44) prior to sunset. Activity levels of owls with radios showed that owls spent <10% of their time in all activity levels (Fig. 2), with <3% in moving activity, mostly involved in foraging. Owls became most active 1 h before and after dark, slightly active shortly prior to dawn, and less active during the day, especially in the morning. Comparisons of daytime versus nighttime activity ratios showed that the daytime proportion of all activities in a 24-h period was higher (45%), a result of other non-moving activities such as preening by day, than that of moving activity (28%). Ali and Ripley (1969) reported Tawny Fish Owls as crepuscular and partially diurnal in habit. In our study, the owls became most active shortly before dark and engaged in intensive foraging until about 1 h after dark. Martin (1990) considered this twilight foraging activity to be more appropriately regarded as nocturnal in habit. The previous proposed circadian rhythm of Tawny Fish owls may reflect a lack of nighttime observations by earlier workers.

The owls' movement varied seasonally (Table 1). Generally, owl movement seemed to peak both in winter for all four birds and in summer for a pair of breeding birds (male—W503; female—W513) (Kruskal-Wallis test, $\chi^2 = 6.74$, $P = 0.08$) and became less active both in fall and winter for all four birds and in summer for the remaining two non-breeding birds (W508 and W494). Seemingly, the percent of daytime movement during a 24-h period seem to be higher for the breeding birds in summer, whereas it was lowest for non-breeding birds in summer ($P = 0.51$). Tawny Fish Owls moved more frequently in winter, probably due to scare natural food sources at Nanshih Stream (Sun 1996). Further, owls may require higher energy to overcome colder weather conditions. Hamilton (1985) and Stalmaster and Gessaman (1982) indicated that Barn Owls (*Tyto alba*) and Bald Eagles (*Haliaeetus leucocephalus*), respectively, consumed greater amounts of food when air temperature declined. Likewise, increased food needs of breeding birds may account for higher movement of the breeding pair (W503 and W513) in the summer of 1995. Laymon (1988) and Sovern et al. (1994) both found that Spotted Owls (*Strix occidentalis*) regularly hunted during the day when feeding fledged young and were more active at night than non-nesting birds. Additionally, at Sakatang Stream, a foraging male Tawny Fish Owl was often seen by day

TABLE 1

SEASONAL MOVING ACTIVITIES (% OF TOTAL ACTIVITY) AND DAYTIME MOVING ACTIVITIES (% OF TOTAL MOVING ACTIVITY) DURING A 24-H PERIOD OF FOUR RADIO-TAGGED TAWNY FISH OWLS AT NANSHIH STREAM DURING OCTOBER 1994–JULY 1996

Season	Moving activity (%)		Percent daytime activity during a 24-h period		Number of days tracked
	Mean	SE	Mean	SE	
Fall (1994–1995)	0.62	0.51	25.74	4.26	8
Winter (1994–1995)	1.43	0.80	26.88	12.93	12
Summer (non-breeding)[a]	0.67	0.30	19.94	15.60	8
Summer (breeding)[b]	1.34	0.62	30.29	9.86	6

[a] Based on activity of W494 and W508, 1995, and a pair of owls (W503 and W513) and W494, 1996.
[b] Based on activity of a pair of owls (W503 and W513) with two fledged nestlings from late May to August 1995.

flushing from a stream near the nest site while the female incubated. Again, on two occasions, the male was seen foraging in the morning after the female had permanently abandoned the nest with an owlet of about seven weeks of age. Because male owls feed incubating females (Mikkola 1983), it may be difficult for the male Tawny Fish Owl to provide enough food for itself, its mate, and young with only nighttime hunting. The increased energetic costs of foraging may explain why the male had to leave the nest and hunt by day to compensate for its hunger.

When foraging at night, Tawny Fish Owls could move up to 1800 m in one hour, with a mean daily moving distance of 275.1 ± 255.6 m/h (range = 3.3 ± 950.0 m, N = 41). When owls visited fish farms at Nanshih Stream at night, the distance moved was shorter (162.1 ± 203.0 m per hour, range = 3.3 ± 870.0 m, N = 17) than when owls foraged exclusively at the stream, $\bar{X}$ = 342.2 ± 270.0 m per hour (range = 92.8 ± 950.0 m, N = 24) (Mann-Whitney test, P = 0.02). On occasion, owls would just remain close by fish farms for the entire night, giving hungry calls-"whe-". Owls moved less at night when visiting fish farms, suggesting an easily available food resource. Basically, Tawny Fish Owls consume <300 g daily (<12% of its body mass), based on total prey biomass per owl pellet (Sun 1996); hence, foraging on fish farms with large fish, such as California rainbow trout (*Salmo mykiss*), definitely satisfied daily requirements more easily than taking natural prey exclusively. Owls sometimes flew directly to fish farms shortly after dark and became inactive during that night, perhaps because they had enough food to be satisfied.

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YUAN-HSUN SUN, Dept. of Wildlife and Fisheries Sciences, *Texas A&M Univ., College Station, Texas 77843, USA (Present address: Dept. of Wildlife Conservation, National Pingtung Univ. of Sci. and Technology, Pingtung, Taiwan 91207)*; AND YING WANG, *Dept. of Biology, National Taiwan Normal Univ., Taipei, Taiwan 117.* *Received 5 Dec. 1996, accepted 15 May 1997.*

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Food habits of nesting Ferruginous Pygmy-Owls in southern Texas.—Although Ferruginous Pygmy-Owls (*Glaucidium brasilianum*, hereafter referred to as FEPO) are listed as endangered in Arizona and threatened in Texas, only anecdotal accounts exist regarding their food habits (Bendire 1888, Bent 1938, U.S. Fish and Wildlife Service 1994). In conjunction with natural history studies on FEPOs of southern Texas (Proudfoot 1996), we collected data to profile the food habits of this species. We incorporated prey remain analysis, visual observation, and information obtained from video recordings to address several aspects of FEPO food habits (i.e., behavior and diet). However, because of the extreme vari-

ations between sampling techniques (i.e., sampling biases), we did not conduct comparative analyses.

Study area and methods.—We conducted research within a 29,000-ha live oak (*Quercus virginiana*)-honey mesquite (*Prosopis glandulosa*) forest on the Norias Division of the King Ranch, Kenedy County, Texas (26°37′30″ and 26°51′30″N, 97°27′30″ and 97°27′30″W), and within 750 ha of >80-year-old honey mesquite thicket on the Knapp Ranch, located 32 km S.W. of the Norias. The climate is subtropical with 68 cm mean annual precipitation and 24°C mean annual temperature. We collected prey remains from eight FEPO nest sites (two in 1994, three in 1995, and three in 1996) postfledging and analyzed them for identifiable prey species. Identification of prey remains was made using dichotomous keys (Jones and Manning 1992, Chaney 1993), university reference collections, and by consulting mammalogists, herpetologists, and ornithologists from Texas A&M University-Kingsville. Numbers of prey items in remains were estimated using standard procedures (Rosenberg and Cooper 1990). However, our inability to distinguish many insect remains (e.g., wing scales) limited this study. Thus, to avoid distorting the results, speculations on numbers of unidentified insects in prey remains were not recorded.

Observation blinds were established about 4 m from four FEPO nest cavities (two natural, two nest boxes). From blinds, observers recorded species and number of prey items brought to the nest cavity by adults. Because FEPOs are primarily diurnal (Gilman 1909, Burton 1973) observations were made between sunrise and sunset post-incubation to fledging (Marti 1987). To ensure sampling all of the FEPOs daily activity, observations were conducted in 3–4 h intervals that alternated among morning, mid-day, and evening.

Video footage obtained from inside active nest boxes ($N = 2$) was used to enhance food habit studies. Two replacement nest box covers were constructed to house miniature video cameras and a light source. In one replacement cover (19 × 20 × 2 cm), a 1.9-cm-diam hole was drilled through the center and a depression 6.0 × 5.5 × 1.9 cm was hollowed around the hole to house a color video camera (XC-42 Computar, Chugai Boyeki Corp., New York, New York). Two 12 V DC miniature lamps (Archer, Radio Shack, Kingsville, Texas) were then similarly installed 3.9 cm on opposite sides of the camera lens. Similarly, a second replacement cover was drilled in the center and hollowed (3.2 × 3.2 × 1.9 cm) to house a smaller black and white video camera (EM200L38 Computar, Chugai Boyeki Corp., New York, New York). One 12 V DC miniature lamp was installed in the second replacement cover to provide light.

During 1994, infrared phototransistors (Archer, Radio Shack, Kingsville, Texas) powered by a 1.5 V DC battery replaced the miniature lamps as a light source to record night activities. Video camera and light source were protected from weather by sealing the edge of the depression with silicon and attaching another hollowed board over the depression. Video patch cables (Radio Shack, Kingsville, Texas) transferred the video image to Canon A1 Digital cam-corders (Canon Inc., Japan) placed in the blind. The power source (i.e., 12 V car battery) provided >40 hrs of use. Replacement covers were installed on active pygmy-owl nest boxes (one in 1994, one in 1995) 7–10 days before nestlings fledged. Video recordings were analyzed for identifiable prey items and compared to information obtained from visual observations and prey remains.

Results and discussion.—Because the frequency of prey species in a raptor's diet is not directly correlated to its nutritional value (Southern 1954), recent studies have used mean biomass to estimate a prey's dietary importance (Marti 1974, Holt and Leroux 1996). However, if raptors consume more juveniles than adults, or more females than males in sexually dimorphic species, mean biomass estimates will distort nutritional values (Steenhof 1983). In addition, because caloric values (cal/g) may differ significantly between prey species (i.e., Northern Cardinal [*Cardinalis cardinalis*] 6020 cal/g, Northern Mockingbird [*Mimus poly-*

glottos] 5490 cal/g) (Cummins Wuycheck 1971), biomass estimates may not be an accurate interpretation of nutritional value. Therefore, lacking the information (i.e., biomass and caloric values of all FEPO prey items) and resources needed to conduct an intensive diet study, we recorded FEPO feeding behavior, frequency of prey deliveries, and prey species to profile the food habits of this owl.

Results.—Thirty-six prey species from five Classes (Amphibia, Aves, Insecta, Mammalia, and Reptilia) were identified during this study (Table 1). Information obtained from prey remain analysis indicated that mammals, birds, reptiles, and insects respectively, comprised 8.6, 10.5, 22.5 and 58.0% of the FEPO's diet. Information obtained from visual observation indicated birds, mammals, reptiles, and insects respectively, comprised 9.1, 10.3, 18.2, and 62.0% of FEPO prey deliveries. Analysis of video recording indicated birds, reptiles, and insects respectively, comprised 2.3, 7.1, and 89.7% of the FEPO's prey deliveries. Amphibians and mammals comprised <1% of video taped FEPO prey deliveries.

Throughout incubation, and for at least the first week posthatch, observations revealed that males collected all the food for females and young. During incubation, most arrivals at the nest site followed ritualistic behavior. On approach to the nest site, males called with a short series of two or three notes. After alighting on a branch near the nest site the male would repeat the two- or three-noted call, and following the second set of calls the female would emerge from the nest cavity, join the male on his perch, appropriate the prey, and fly off to feed, cache the prey ($N = 3$), or enter the nest cavity. Alterations from this behavior entailed the male entering the cavity to deposit prey, after announcing his approach. On four occasions (once at one nest and three times at another nest), copulation was observed between males and females after food deliveries. On three occasions, 1–4 days pre-fledging, two adult males were observed appropriating large prey items (e.g., Pyrrhuloxia [*Cardinalis sinuatus*]) provided to nestlings by adult females.

At three weeks posthatch, both adults were observed bringing prey into the nest site, however, adult males were not recorded distributing meals of prey to nestlings. Video recordings showed three peak activity periods: 07:30–08:30, 14:30–15:30, and 19:30–20:30 (Fig. 1). Analysis of video recordings indicated intense brood competition over prey items deposited by adults and over meals disbursed by adult females. In one nest that hatched five eggs, brood competition resulted in siblicide of the youngest and smallest nestling at 18 days posthatch.

Discussion.—Our results were similar to those reported by Solheim (1984) for Eurasian Pygmy-Owls (*Glaucidium passerinum*) and support anecdotal accounts of FEPO feeding behaviors (Johnsgard 1988); FEPOs are generalistic predators. In addition, cataloging hispid cotton rat and Eastern Meadowlark (*Sturnella magna*) in the diet of FEPOs lends validity to anecdotal reports of FEPOs taking prey larger than themselves (Bendire 1888, Bent 1938). Information obtained from analysis of video recordings (i.e., time of prey deliveries) substantiates anecdotal reports that FEPOs are primarily diurnal foragers (Bent 1938). We hypothesize that the peak activity periods in FEPO prey deliveries may be the effect of prey behavior and nutritional need. In the early morning hours, passerines are preoccupied with courtship and feeding, diurnal reptiles and insects emerge from cover and enter open areas to thermoregulate, and small mammals become conspicuous, increasing susceptibility to predation. Coincidentally, because FEPOs were not recorded feeding at night, we hypothesize that the nutritional needs of FEPOs may be at their peak in early morning. Hence, increased prey susceptibility coincides with nutritional need of FEPOs. Thermoregulation and nutritional requirements may contribute to the mid-afternoon peak in FEPO prey deliveries. Although many birds and small mammals seek cover in the mid-day heat of southern Texas, diurnal reptiles and insects in the forest increase their foraging activity to meet increased metabolic requirements. Consequently, mid-day foraging of reptiles and insects

TABLE 1

NUMBER OF PREY ITEMS FOUND IN THE DIET OF NESTING FERRUGINOUS PYGMY-OWLS IN SOUTHERN TEXAS, SPRING 1994, 1995, AND 1996

Prey	Number and Frequency of Prey Identified[a]					
	PR	%	VO	%	VR	%
Narrow-mouth toad (*Gastrophryne olivarea*)	0	0.0	0	0.0	1	tr.
Bewick's Wren (*Thryomanes bewickii*)	2	1.0	0	0.0	0	0.0
Blue Grosbeak (*Guiraca caerulea*)	1	tr.	0	0.0	0	0.0
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	4	2.0	0	0.0	0	0.0
Eastern Meadowlark (*Sturnella magna*)	1	tr.	1	1.3	0	0.0
Pyrrhuloxia (*Cardinalis sinuatus*)	3	1.4	2	2.6	2	1.6
Nashville Warbler (*Vermivora ruficapilla*)	0	0.0	1	1.3	0	0.0
Northern Cardinal (*Cardinalis cardinalis*)	1	tr.	0	0.0	0	0.0
Northern Mockingbird (*Mimus polyglottos*)	1	tr.	0	0.0	0	0.0
Cicada (Cicadidae)	0	0.0	1	1.3	0	0.0
Click-beetle (Elateridae)	6	2.9	0	0.0	0	0.0
Cone-nosed blood sucker (Reduviidae)	9	4.3	0	0.0	2	1.6
Dragonfly (Aeshnidae)	0	0.0	0	0.0	1	tr.
Grasshopper (Acrididae and Tettigoniidae)	102	48.8	15	19.5	77	61.1
Lightning bug (Lampyridae)	3	1.4	0	0.0	0	0.0
Preying mantis (Mantidae)	0	0.0	0	0.0	1	tr.
Round-headed katydids (Phaneropterinae)	1	tr.	0	0.0	3	2.4
True katydids (Pseudophyllinae)	0	0.0	5	6.5	7	5.6
Walking stick (Heteronemiidae)	1	tr.	0	0.0	0	0.0
Common evening bat (*Nycticeius humeralis*)	1	tr.	0	0.0	0	0.0
Hispid cotton rat (*Sigmodon hispidus*)	2	1.0	2	2.6	0	0.0
Hispid pocket mouse (*Chaetodipus hispidus*)	0	0.0	2	2.6	0	0.0

TABLE 1
CONTINUED

Prey	Number and Frequency of Prey Identified[a]					
	PR	%	VO	%	VR	%
House mouse (*Mus musculus*)	1	tr.	0	0.0	0	0.0
Northern pygmy-mouse (*Baiomys taylori*)	7	3.3	0	0.0	0	0.0
Texas kangaroo rat (*Dipdomys compactus*)	3	1.4	2	2.6	1	tr.
Four-lined skink (*Eumeces tetragrammus*)	2	1.0	0	0.0	0	0.0
Ground Skink (*Scincella lateralis*)	6	2.9	8	10.4	4	3.2
Great plains skink (*E. obsoletus*)	3	1.4	0	0.0	0	0.0
Keeled earless lizard (*Holbrookia propinqua*)	2	1.0	0	0.0	0	0.0
Rose-bellied lizard (*Sceloporus variabilis*)	7	3.3	1	1.3	0	0.0
Six-lined racerunner (*Cnemidophorus sexlineanius*)	2	1.0	0	0.0	0	0.0
Texas horned lizard (*Phrynosoma cornutum*)	2	1.0	0	0.0	0	0.0
Texas spiny lizard (*S. olivaceus*)	9	4.3	0	0.0	3	2.4
Texas spotted whip-tail (*C. gularis*)	1	tr.	0	0.0	1	tr.
Unidentified insects	NR	NR	27	35.1	22	17.5
Unidentified reptiles	13	6.2	5	6.5	2	1.6
Unidentified mammals	3	1.4	2	2.6	0	0.0
Unidentified birds	9	4.3	3	3.9	1	tr.

[a] PR = prey identified from remains obtained from eight Ferruginous Pygmy-Owl nest cavities; VO = prey identified from visual observation at four Ferruginous Pygmy-Owl nest sites, included 105 h 4 min of viewing; VR = prey identified from analysis of video recordings obtained from inside two active Ferruginous Pygmy-Owl nest boxes, included 104 h 3 min of video footage; tr. = trace; NR = not recorded.

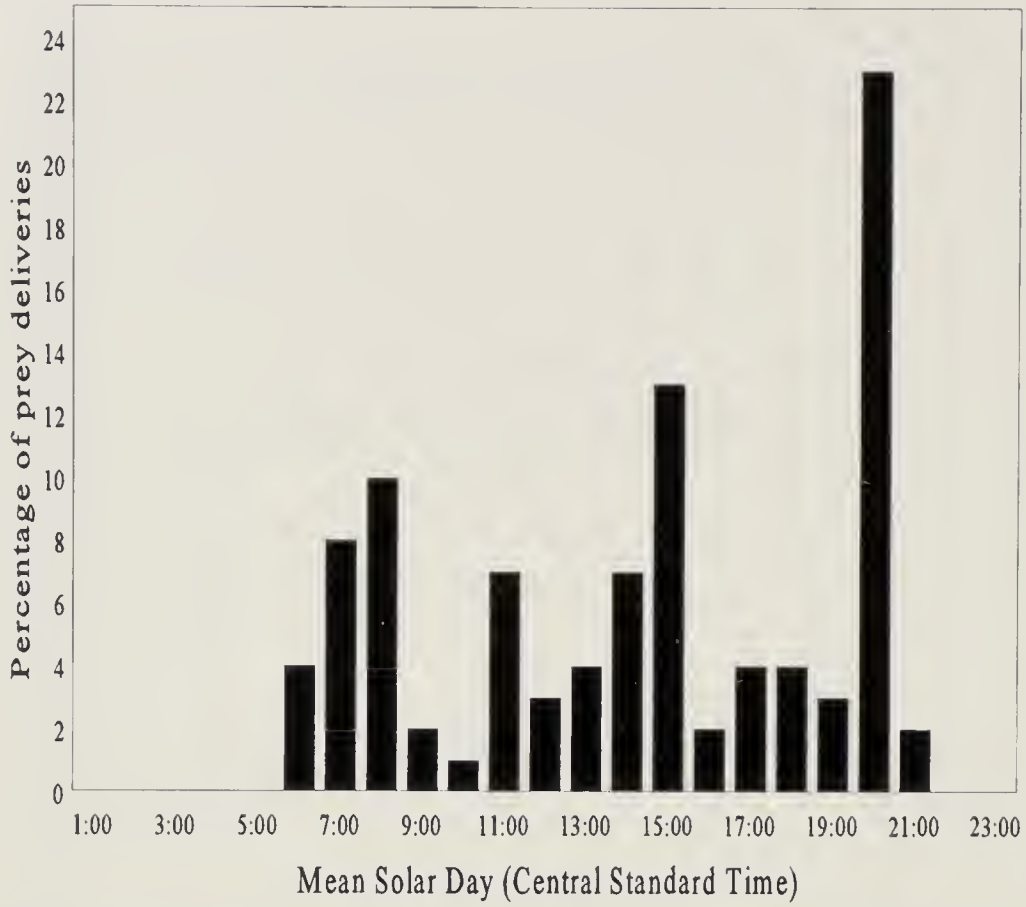

FIG. 1. Daily feeding activity at one Ferruginous Pygmy-Owls nest site in southern Texas, based on analysis of 48 h of video recording and prey deliveries.

increases their availability and susceptibility to predation. With a readily available food source, FEPOs may forage at libitum to meet mid-afternoon nutritional needs. Another hypothesis regarding afternoon peak activity may entail prey caching. FEPOs may execute excessive foraging during early morning hours and cache prey to meet mid-afternoon nutritional needs. We hypothesize that the evening peak may be attributed to the emergence of small mammals during periods of dim light, increasing availability and susceptibility of prey to predation; reductions in visual acuity of birds, reptiles, and insects in dim light, increasing susceptibility to predation; and the increased nutritional need of sustaining a brood of FEPOs through the night.

As both a primary and secondary food source (i.e., food for FEPOs and FEPO prey [passerine birds and lizards]), insects may play a pivotal role in the diet of FEPOs, although caloric values are unknown. The drought of 1995 resulted in drastic reductions in large insect (i.e., Orthoptera) numbers on the study area between 1995 and 1996 (pers. obs.). This coincides with reductions in FEPO hatching, fledging, and production efficiency (i.e., all fledglings/all eggs) (Proudfoot unpubl. ms). Although coincidental occurrence could account for these reductions, the possible negative affect of reduction or elimination of a single prey class in the diet of FEPOs warrants consideration.

This study emphasizes the importance of multifaceted food habit studies by demonstrating the significance of prey remains analysis and the benefits video recordings and visual observations have in obtaining behavioral information (e.g., brood competition, adults appro-

priating prey from nestlings to initiate fledging, and prey caching). Solheim (1984) recorded Eurasian Pygmy-Owls in Norway caching prey in nest cavities during winter and attributed this behavior to their small body size and higher metabolic rates relative to other owls. In addition, Solhiem (1984) hypothesized caching and retrieval of prey items suggests extended memory and possibly learned behavior. Because we observed similar behavior in FEPOs, this information may benefit future evolutionary studies of this species.

To conclude, our results suggest that FEPOs are generalistic predators and may not be influenced by the availability of any single species. However, this study failed to address areas of research (i. e., significance [caloric value] of prey species in the diet of FEPOs) essential for describing the impact of forest and resource management practices on this species. Therefore, before management guidelines are drawn, we suggest a more intensive FEPO diet study be conducted.

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GLENN A. PROUDFOOT, *Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, Texas 78363*; AND SAM L. BEASOM (deceased) *Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, Texas 78363.* *Received 19 Nov. 1996, accepted 21 April 1997.*

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The significance of fishing by Northwestern Crows.—Fishing by crows has been reported anecdotally in a few cases, specifically in the Carrion Crow (*Corvus corone*) (Dunn 1985) and Northwestern Crow (*C. caurinus*) (Shepherd 1988). We describe here the behavior in greater detail and suggest that intertidal zone fishing provides a significant source of nutrition to Northwestern Crows during limited, but predictable foraging periods. On two occasions we have observed large groups of Northwestern Crows fishing systematically for Pacific sand lances (*Ammodytes hexapterus*) buried in sandy areas at very low tides.

The first observations were made on 25 August 1996 between 08:08 and 08:45 PST at Meadowdale Park Beach, north of Seattle, Washington on Puget Sound. The tide height ranged from .03 m above to −0.2 m below mean low tide during this period. The birds demonstrated a distinctive behavior of flipping sand to each side with their beak while digging a 5–8 cm hole in the sand. This usually resulted in the bird pulling out a silvery slender fish approximately 150 mm in length. The birds held the fish sideways in their bills initially, then set the fish on the sand, reoriented the fish lengthwise and swallowed it whole. This behavior was observed in the majority of birds on the beach at that time, numbering from 36 to 41. Three specific birds were observed for 10 minute focal samples, documenting their behavior both prior and subsequent to the capture of one of these fish. These observations indicated that a crow could find and handle a fish in less than five minutes. One of those three birds lost its prey to a conspecific: scrounging (intraspecific theft [Vickery et al. 1991]) was observed at high rates during periods of fishing. Gulls also took sand lances from crows and were never observed digging for the fish themselves.

The second observation period was on 28 August 1996 between 10:20 and 11:23 PST at Meadowdale Park Beach. The tide height during this period ranged from 0.1 m above to −0.3 m below mean low tide. Again, a large majority of the 28 birds on the beach were observed to perform this behavior, though it only occurred in this narrow window of time and tide height. We observed 12 "scrounges" of sand lances during this period. Again, gulls took fish from crows and were not observed searching or digging for fish.

We eventually obtained one of the fish by running up to birds who were digging but had not yet obtained their fish. This sample was confirmed as a Pacific sand lance (*Ammodytes hexapterus*). The high rate of both intra- and interspecific theft suggested to us that the sand lances were highly valued by both crows and gulls. We were particularly interested in the value of a fish in satisfying a crow's daily energy requirements. The average daily energy requirement of a 285g crow (Pyle et al. 1987) can be estimated at 403.7 kJ/day (Walsberg 1983). The average length of a sand lance is 15.5 cm with a caloric content of 22.52 kJ/g-dry weight (Vermeer & Devito 1986). We converted the average length into wet weight (Vermeer & Devito 1986) and converted wet weight to dry weight (0.29 g-dry/g-wet; Cooper 1978). This resulted in a value of 120.1 kJ/fish. In a similar fashion, the energy content of intertidal worms, a frequent intertidal food item (pers. obs.), (average dry-weight: 25mg) was calculated to be 0.42 kJ/worm (Goss-Custard 1977a, 1977b). Thus, the average crow needs only 3.4 sand lances/day to satisfy their daily energy requirements, whereas they would need 961.2 average-sized worms. Clearly these fish provide a valuable energetic

resource. However, the fish are only available bimonthly at the lowest tides (Shepherd 1988). In our study area, these lowest tides (<0 m) occur for 4–8 successive days and last approximately 30–60 minutes each day.

From a more general point-of-view, this resource is unusual in that it is highly valuable and limited, but predictable in its temporal distribution. Most food resources that are highly rewarding and of limited duration are unpredictable in their occurrence (e.g., insect molting swarms). Perhaps this unusual combination of characteristics explains why the resource produces such intense intra- and interspecific competition and has been exploited by crows (and through the foraging abilities of crows, other predators) in both the Kodiak Archipelago (Shepherd 1988) and the Puget Sound region.

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Renee L. Robinette and James C. Ha, *Dept. of Psychology, Univ. of Washington, Box 351525, Seattle, Washington 98195.* *Received 28 January 1997, accepted 19 August 1997.*

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Long-term memory of an auditory stimulus for food in a natural population of the Mexican Jay.—The role of learning and memory in the development of foraging skills should be especially important in species that utilize a wide variety of food, as do many members of the family Corvidae (Goodwin 1976). Jays and other corvids can be easily conditioned in the laboratory to respond to various kinds of stimuli (usually visual) that signal the probable presence of food (Pietrewicz and Kamil 1981). For natural populations it is common knowledge that birds learn the locations of food and feeders, and experimental evidence of memory of locations of food is available (Kamil and Balda 1990, Shettleworth

1990). However, evidence for the learning and long term memory of auditory stimuli associated with food under natural conditions has received little attention (Kamil and Roitblat 1985, Kamil 1989). This note describes evidence for a long term memory of an auditory stimulus and suggests a mechanism for its cultural transmission.

The observations were made during a long-term study on a color-banded population of the Mexican Jay (*Aphelocoma ultramarina*) at the Southwestern Research Station of the American Museum of Natural History in the Chiricahua Mountains of Arizona. A review of the behavior and ecology of this population and a description of the study area may be found elsewhere (Brown and Brown 1990, Brown 1994).

From 1979 through 1994 my colleagues, assistants and I studied dominance interactions at bait stations in up to ten flocks of the Mexican Jay in winter (Barkan et al. 1986, Craig et al. 1982). After a few seasons of observation we suspected that the jays were associating the investigator's arrival at the observation station with food, since some would fly to the site and call when they saw one of us coming. Moreover, some individuals would occasionally spread their wings in a begging posture as the observer approached. To begin observations a small amount of food was put out by the observer to induce dominance interactions. The food was generally gone by the end of the observation period.

To test the hypothesis that the jays would learn to associate a simple auditory stimulus with food we blew a "police whistle" a few times just before putting out the food. It did not take long for each flock to learn this association. It would come to the whistle even when the flock was far away and out of sight. After training it was only necessary for us to blow the whistle once or twice to elicit a response from the jays. A response invariably began with some calling, wherever the jays were at the time. Then the flock, or part of it, would fly directly to the bait site and land in the surrounding trees, calling in flight and after alighting. The response seemed to fail in two situations, (1) when a flock was beyond hearing range for the whistle, as on windy days or when they were far away on the other side of a hill, or (2) when they were in imminent danger from a nearby accipiter hawk. We soon came to depend upon the whistle to bring in our subjects whenever we wanted to observe them or trap them.

The jays responded to the whistle not only in winter, but also during the breeding season and in warm weather, especially in drought years when food was short. The usual interval between observation sessions in winter was three to five days. In the winter of 1991–92, however, we did not study dominance, and we were not present on the study area. Soon after I arrived at the study area, 13 March 1992, I tested the hypothesis that the jays would respond to the whistle in the usual manner on the first trial, without any experience with the whistle at bait stations since June 1991, an absence from the conditional stimulus of eight and a half months.

The test was simple. For each of ten flocks I blew the whistle in the usual way at the bait site. I then observed whether some birds called and approached in the next two minutes. Eight of the ten flocks met this criterion. Usually some birds called in the distance within a few seconds and the flock began to appear. Typically all or most of the flock came. In the spring of 1992, however, there were 39 jays on the study area that had hatched in 1991 and were, therefore, inexperienced with the whistle stimulus and seed reward. These naive individuals did not respond to the whistle in the first few days of exposure to it. There were also several recent, unbanded immigrants to the study area, who presumably had little or no such experience. Since the older, longtime residents on the territory probably led the flocks, the inexperienced members would quickly be exposed to the reward if they followed the flock. In spring 1992, since yearlings had not been trained directly during the preceding winter months, their introduction to the whistle-seed association must have been first learned from older members of their flock. Cultural transmission from older and experienced to

inexperienced flock members could, therefore, have occurred. Direct, non-cultural learning could also have occurred, but it would have followed and been facilitated by the responding behavior of experienced older birds. In some flocks there were individuals who responded consistently to the whistle and others who disregarded it altogether. Thus although a flock often responded more or less as a unit it was clear that there was variation among individuals.

In 1997 the same procedures were followed. At all eight flocks tested the jays responded by calling. The latency to first call was 1–2 sec for six flocks and 8 sec for two. In seven flocks some flock members flew directly to the bait site last used in June 1995.

Although each flock was trained with the same whistle, it responded only in its own territory and typically flew to its habitual feeding site where the whistle was blown in its own territory. This site-specificity is easily explainable on the basis of the territorial behavior of the birds and the difficulty of hearing the stimulus in other territories. In 1996, however, some individuals of one flock responded to the whistle in a neighboring flock. These individuals would sneak in while the home flock was absent. Jays in untrained flocks are not attracted to the sound of a police whistle. In spring before the first tests we did not make systematic observations, but birds in trained flocks rarely visited the bait site in the absence of the whistle or of bait; hours or days might pass before seeing one visit the site. We did not systematically record data on the frequency of visits.

Although social learning in the traditional sense (Zentall and Galef 1988, Heyes and Galef 1996; Nicol and Pope 1994) is not proven by these observations, they are consistent with the social foraging habit in this species and with a previous report of "communal harvesting of a transient resource" (Brown 1983). Although many cases of "socially transmitted foraging behavior" have been reported (Lefebvre and Palameta 1988), none describes the use and possible cultural transmission of a conditioned auditory cue.

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JERRAM L. BROWN, *Dept. of Biological Sciences, State Univ. of New York, Albany, New York 12222.* *Received 11 February 1997, accepted 30 June 1997.*

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ORNITHOLOGICAL LITERATURE

EDITED BY WILLIAM E. DAVIS, JR.

ECOLOGY, CONSERVATION, AND MANAGEMENT OF COLONIAL WATERBIRDS IN THE MEDITERRANEAN REGION. By Alain J. Crivelli, Heinz Hafner, Mauro Fasola, R. Michael Erwin, and Donald J. McCrimmon, Jr., editors. Colonial Waterbirds 19 (Special Publication 1). 1996: 227 pp., 1 black-and-white drawing, 59 figs., 64 tables. $30.00 (paper).—The conservation of wetlands and their associated flora and fauna is a problem of international concern. Efforts to protect and manage the wetlands of the Mediterranean basin and the waterbirds that they support have resulted in some of the most detailed, long-term research studies and conservation models anywhere in the world. Several international symposia thematically dedicated to wetland and waterbird conservation and management have been convened during the last two decades and these have had great impact both politically and ecologically. For example, Mediterranean biologists have successfully established 89 Ramsar wetland sites and most countries in the basin are cosignatories to the Ramsar Convention, an international agreement to designate and protect wetlands of special ecological value. Much credit for the wetland conservation efforts in the Mediterranean basin must be given to the director and biologists of the Station Biologique de la Tour du Valat who not only have initiated many research efforts but also have provided training and guidance to wetland researchers from many countries in the basin. It was no accident, then, that the Colonial Waterbird Society chose to sponsor a "Mediterranean Symposium" in Arles, France, as a part of their annual conference in October, 1993. This publication, the product of the symposium, focuses primarily upon the breeding biology and feeding ecology of waterbirds in the Mediterranean region.

The symposium provided biologists from many countries with an opportunity to exchange information on the population trends and current status of species, ecological problems common to large areas of the region, the biology and ecology of wetland birds, and conservation and management strategies. The resulting proceedings provides a thorough overview of the state of wetland and waterbird research in the Mediterranean basin. Eighteen oral presentations and 27 poster papers were presented at the meeting, and 25 of these offerings were converted to the written papers that comprise this publication. The papers were contributed by 47 individual authors representing 10 countries. Not surprisingly, not all of the papers included in the volume are as scientifically rigorous as one might expect, but all are well prepared and presented. Given the difficulties that they must have faced with translation and communication, the editors should be heartily congratulated for producing a volume that is both well-written and editorially sound.

The first two papers in the volume provide a complete synthesis of wetland and waterbird conservation efforts in the region, both past and present, and they are particularly well-written. The first paper, authored by R. Michael Erwin, provides both an ecological overview and a shopping list of conservation needs. Luc Hoffman, Heinz Hafner, and Tobias Salathe follow this with a summary of the history of waterbird research in the Mediterranean basin and they describe how some of the research projects developed into long-term ecological programs. These authors conclude the paper with a discussion of how current research efforts can be made relevant for conservation.

The other 23 papers in the volume can be classified loosely into four topical categories. As might be expected in some countries where ecological research is in its infancy, many papers (six) are devoted to assessments of waterbird population statuses and trends. Ten of

the papers focus on the feeding ecology of species, four describe breeding biology, and the remainder examine conservation efforts or describe special ecological conditions. There was no apparent attempt on the part of the editors to organize the papers by taxa, topic, or country. However, this apparent lack of organization is mostly superficial because most papers contain information on several taxa and most have some direct application to conservation efforts. Three papers that describe the use of rice fields by waterbirds are presented consecutively and these papers may be of considerable interest to biologists in the rice belt of the United States and elsewhere. Since the conservation planning and research needs in the Mediterranean region seem to have many parallels in other regions of the world, most papers in the volume contain information or consider approaches that may be relevant to other scientists.

Unlike many symposium volumes, this one is rendered more useful by the inclusion of an index. The index, prepared by Annmarie L. Stepp, contains page references by country, key words, scientific names, vernacular names and authors. The volume itself is dedicated to Luc Hoffman, the 1994 recipient of the Colonial Waterbird Society's Kai Curry-Lindahl Award for Conservation, for his lifelong efforts on behalf of wetland and waterbird conservation and management in the Mediterranean region.

This Special Publication should be of especial interest to ornithologists and conservation biologists interested in wetland and waterbird ecology and management both in the United States and abroad. The Colonial Waterbird Society (CWBS) should be commended for providing the opportunity for the international symposium and for making the proceedings available to a wide audience. The Special Publication, which was provided to all CWBS members and subscribing libraries, may be purchased directly from the CWBS Treasurer by non-members. Orders for the volume should be directed to A. Larry Bryan, Savannah River Ecology Lab, Drawer E, Aiken, SC 29802, USA. The price includes shipping and handling.—Brian R. Chapman.

Raptors in Human Landscapes: Adaptations to Built and Cultivated Environments. Edited by David M. Bird, Daniel E. Varland, and Juan J. Negro. Academic Press, New York. 1996: 396 pp., 46 figs., 65 tables, 5 app. $72.00 (cloth).—Recent estimates suggest that at least 40% of our planet's terrestrial surface has been altered by human activity. Thus, it should come as no surprise that—with the possible exception of a few restricted-range tropical endemics—at least some populations of all raptors currently inhabit human-modified landscapes. This book, the proceedings of a symposium on raptor adaptations to human landscapes that was held at a Raptor Research Foundation meeting in Charlotte, North Carolina, in November 1993, successfully introduces the reader to most of the traditional methods scientists and conservationists have used to study how such cohabitation affects these birds.

The book is divided into five sections: raptors in urban landscapes (nine papers), raptors and artificial nest sites (eight papers), raptors in cultivated landscapes (nine papers), raptors in industrial landscapes (four papers), and raptors at large (four papers). Most of the contributions represent synoptic, well-referenced overviews of recently completed or ongoing studies. Although the book has a decided North American flavor, there are papers from authors residing in England, India, Mexico, Scotland, Spain, Tasmania, and Zimbabwe. All but two of the contributions present the results of species- or site-specific studies. There is little in the way of regional or continental assessment, let alone a global overview.

Although details differ considerably among studies, the general conclusion is that, so long as uncontaminated food is abundant, safe nesting sites are available, and direct persecution

is minimal, most temperature raptors are capable of surviving in extensively modified habitats. Whether the same is true for forest-dependent tropical raptors remains to be seen. Also unclear, and, unfortunately, largely undiscussed, is the extent to which human-induced modifications in landscapes are modifying the behavior and ecological function of the raptors inhabiting them. In eastern North America, for example, many Red-tailed Hawks (*Buteo jamaicensis*) currently feed extensively on "road kills," especially in winter. The extent to which this relatively recent shift in prey availability has affected the species' migratory habits, as well as its role as a predator, remains unknown. Also largely unstudied, is the extent to which recent increases in the numbers of bird feeders in North America are affecting winter survival in Sharp-shinned (*Accipiter striatus*) and Cooper's (*A. cooperii*) hawks, and how this, in turn, may be affecting the ecology of these species, as well as the species with which they interact. Studies of the effects of human-modified landscapes on raptors desperately need to move beyond reactive, raptor-focused investigations of reproductive success and population change, and into the realm of more systematic, comparative studies of how human activity affects raptors as ecological entities.

Even though the book presents many more questions than it answers, the editors are to be congratulated for bringing together and successfully publishing the state-of-the art in the early 1990s. Clearly, the work offers fertile grounds for ideas for many graduate student theses, as well as for more extensive long-term studies. My principal concern is that the book's rather steep price will limit its distribution and, therefore, use.—KEITH L. BILDSTEIN.

FERAL PIGEONS. By Richard F. Johnston and Marián Janiga. Oxford Univ. Press, New York and Oxford. 1995: xvi + 320 pp., 67 figs., 60 tables. $95.00 (cloth). ISBN 0-19-508409-8.—Johnston and Janiga's "Feral Pigeons" offers a complete guide to the biology of feral pigeons. Feral pigeons are not just "domestic" birds on the loose; neither are they wild birds (Rock Doves [*Columbia livia*]) once tame. Rather, feral pigeons, as the authors take pains to define and explain, exist as populations with unique and varied phylogenies. Feral pigeons have had a history of artificial selection as domestics, but now—as captives no longer—are under more "natural" natural selection. Ordinary people may not be impressed with the pigeons they see, but Johnston and Janiga see them as "superdoves" with many virtues for their study. This book persuasively presents these virtues. For an overview, the preface recommends approaching the text by means either of Chapter 1 ("first things first") or Chapter 23 ("first things last"). Chapter 1 discusses origins. Rock Doves were the wild progenitors of domestic pigeons; escaped domestics began feral populations which continued more or less genetic contact with wild Rock Doves. Chapter 23 looks again at pigeon-human relationships. In between are chapters summarizing many facets of pigeon biology: chapter 2 discusses morphology and genetics; chapters 3–10 summarize breeding biology (from pair formation, nest, eggs, incubation, hatching, and nestling growth); the remaining chapters include a variety of topics: diet, plumage polymorphism, molt, flight, navigation, population biology, and population control. I appreciated the pencil drawings of Peter Trembáč. The literature cited section is 28 pages long and includes many references from eastern European sources. Of necessity, the literature gives guidance to that of domestic and wild Rock Doves as well. Richard F. Johnston came to this book from studies of feral pigeons at Lawrence, Kansas. Marián Janiga brought his experience with the feral pigeons of Bratislava, Slovakia. Together they provide a world view of feral populations of Rock Doves—PETER E. LOWTHER.

ANTBIRDS AND OVENBIRDS: THEIR LIVES AND HOMES. By Alexander F. Skutch, illus. by Dana Gardner. University of Texas Press, Austin, Texas. 1996: 268 pp., 16 black-and-white photos, 55 line drawings, 6 tables. $40 (cloth), $19.95 (paper).—Like many of Alexander Skutch's books, this one is a nice blend of personal observations accumulated over six decades and a distillation of the literature about the focal birds. Only two chapters represent modified versions of previously published work. This book deals with two of the largest South and Central American bird families, the antbirds (Formicariidae) and ovenbirds (Furnariidae), the former with roughly 250 species, the latter with about 215 (Skutch does not comment on the recent splitting of the antbirds into two families, the typical [Thamnophilidae] and ground [Formicariidae] antbirds or making the woodcreepers a subfamily of the Furnariidae). Antbirds are treated in the first eleven chapters, ovenbirds in the last ten. The first seven chapters of each section are parallel, dealing with a general description of the family; food and foraging; daily life; voice, displays, and courtship; nests; eggs and incubation; and young and their care. The eighth chapter details a single species. The accounts diverge at this point, with chapters nine and ten in the antbird section dealing with nesting success, breeding seasons, and survival, while in the ovenbird section a single chapter deals with enemies, nest success, and survival. Each section concludes with a chapter on the interactions of the family with humans. The pages ring with the names of interesting sounding birds—fire-eye, bare-eye, gnateaters, spinetails, thistletails, tuftedcheek, softtails, prickletails, barbtails, wiretails and brushrunner.

In the Foreword, David Snow states that the book is "full of gems of observation and description" and that one of Skutch's attributes has been to describe his observations "in a style full of fluency and grace." I agree. We not only learn about army ant biology and that there are 28 species of antbirds which are considered "professional" (obligate) army ant followers but read vivid descriptions of antbirds foraging with ant columns and swarms, using the ants as beaters. We learn that the Bicolored Antbird's (*Gymnopithys leucaspis*) voice is "Pleasantly whimsical rather than musical," that in displays "the same embellishments are conspicuous in both agonistic encounters and in courtship—they cannot change their clothes for different occasions." One ovenbird sings as "the shadows of night descend through clouds of foliage." He captures the essence of the birds, e.g., antpittas "are roly-poly birds with legs that seem too long for them and tails too short." Much of the text is descriptive, but there are frequent ecological comparisons such as of antwrens filling the ecological role of warblers of temperate forests, or hypotheses, e.g., that bare skin around the eyes may be advantageous to birds which forage in dense vegetation. Skutch also broaches broad philosophical questions, many of which have strong anthropomorphic implications—do antbirds feel love or affection for mates, anger, genuine distress, or fear? Skutch concludes that empathy suggests that they do but that science "remains stubbornly silent," and speculates on the importance of the answers to these questions. He states that spinetails and thornbirds (which construct elaborate stick nests) appear to take "pride in their housekeeping, and seem to *enjoy* building and maintaining their nests, which may be the reason why they make them so elaborate." These and other philosophical and metaphysical speculations may irritate some readers but do not detract from the careful and patient natural history observations which form the heart of this book. Skutch's writing is very personal—he takes the reader to the rainforest and makes the birds come alive—my favorite story in this book is about a Bicolored Antbird, "Jimmy," that used Skutch as a beater on many occasions for more than a year, following him and snapping up insects which Skutch disturbed.

The illustrations by Dana Gardner beautifully complement the text. There are no in-text references, a compromise to readability no doubt, but Skutch always credited other's work by name and a search of the bibliography usually turned up an unambiguous reference

(occasionally there were several papers by the same author and it was not entirely clear which one contained the information mentioned in the text). But this is a minor quibble. The book is informative and delightful natural history reading. I recommend it to anyone who plans to visit the New World tropics or study its birds.—WILLIAM E. DAVIS, JR.

THE NATURE OF MASSACHUSETTS. By Christopher Leahy, John Hanson Mitchell, and Thomas Conuel, illus. by Lars Jonsson. Massachusetts Audubon Society, Lincoln, Massachusetts, and Addison-Wesley Publishing Co., Reading, Massachusetts. 1996: 226 pp., 126 field sketches in pencil and watercolor. $40 (cloth).—This book was published as part of the celebration of the 100th anniversary of the founding of the Massachusetts Audubon Society. It focuses on the natural history of Massachusetts and is much more than the usual coffee-table book. The first of three sections, entitled "The Founding Mothers," presents the highlights of the history of the Massachusetts Audubon Society. In 1896 two Boston Brahmins, Harriet Hemenway and Minna Hall, began to organize a fight against the slaughter of birds for the millinery trade and soon recruited William Brewster, a founder of the Nuttall Ornithological Club and the American Ornithologists Union, as the first president of the fledgling Massachusetts Audubon Society (MAS). They also secured the support of a number of other prominent ornithologists, including Edward Howe Forbush, George Mackay, and Outram Bangs, and made Charles S. Minot the chairman of the board. The organization soon became a national activist, distributing legislation models and leaflets. This activism was influential in the formation of other state organizations and what would eventually become the National Audubon Society. The broadening of the focus from birds to natural history in general and the eventual focus on habitat preservation, both in Massachusetts and internationally in Belize and Costa Rica, rounds out the historical perspective. The second section, and bulk of the book, is a guide to the natural communities of Massachusetts. The state is divided into four sections and 23 natural communities (e.g., salt marsh, Atlantic white cedar swamp, oak-conifer forest). An informative discussion of the ecology of each community is followed by a list of plant and animal indicator species (including birds), the distribution of the community world-wide and in Massachusetts, conservation status, a list of places to visit in the state, and suggested readings. Scattered throughout the text are the attractive drawings and paintings by Lars Jonsson, nearly half of which feature birds. The illustrations range from rough pencil sketches to finished watercolors, and capture the essence of the natural communities that they illustrate. The final section of the book focuses on the 31 MAS wildlife sanctuaries. For each sanctuary there is a description of salient features (e.g., 200 miles of trails, 66 nesting bird species), directions, and telephone numbers. Appendices include a "Resources" section which provides a list of field guides, other relevant books, periodicals, maps, conservation organizations, clubs and programs, museums and "living collections," and governmental conservation agencies and programs. A glossary defines nearly fifty terms commonly used in the text (e.g., lentic, oligotrophic, riparian), and the thorough index provides the scientific names of all genera and species mentioned in the text.

This book has more than local or regional interest because of the role that MAS has historically played in conservation on the national and international level. I recommend this beautifully illustrated book to anyone interested in the history of the conservation movement or who enjoys well-written accounts of natural communities. It is, however, more about the places where birds live than about the birds themselves. Certainly, anyone visiting Massachusetts would find this book useful.—WILLIAM E. DAVIS, JR.

A NATURALIST ALONG THE JERSEY SHORE. By Joanna Burger. Rutgers Univ. Press, New Brunswick, New Jersey. 1996: 304 pp., 97 line drawings, 6 maps. $18.95 (paper); $40 (cloth).—This is a book of essays about the plant and animal communities of the New Jersey shore but has a broader perspective because many of the organisms described have extensive ranges. Hence, the book should be of interest to anyone curious about shore life from Maine to Florida—or shore life anywhere. Four introductory chapters deal with the origin of the shore and its biotic communities, birds on the salt marshes and beaches, a variety of commercial ventures (including mosquito ditching and pesticide problems), and the potential threats to the shore from global climatic change. The remaining 24 chapters follow a single cycle through the seasons, and each features a particular animal subject (about two-thirds of the chapters feature birds). In spring, we read of oystercatchers and willets, the Fowler's toads and their spring chorus, killifish, and horseshoe crabs on Delaware Bay. In summer we read of terns and skimmers, diurnal predator ghost crabs, mink and mussels, diamondback terrapins, and the New Jersey State Bird: the mosquito. In fall, the shorebirds return, and we follow migrating hawks and monarch butterflies at Cape May. We read of winter solitude, geese and brant at Brigantine and Barnegat Bay, and come full cycle to the harbingers of spring, Killdeer on the Rutgers campus, and gulls, herons, and egrets. Birds figure in some way in most chapters. The book reads easily, although a stronger editorial hand would have eliminated the occasional redundancies (e.g., we learn that fiddler crabs have burrows as deep as 35 inches twice in two pages), but this is a minor problem. This is very personal narrative by an author who has spent thousands of hours watching the plants and animals she describes. It is laced with appealing imagery—e.g., the chapter on horseshoe crabs begins, "A sea of dark brown shapes agitates the shallow water, giving the impression of intense fermentation, a massive pot of coffee coming to a boil." The drawings from her sketch pads add another personal and effective dimension. This book is clearly a labor of love, nicely written, informative, and a pleasure to read. A strong conservation message is implicit or explicit throughout. I highly recommend it to for anyone for whom the smell of salt air has a special meaning.—WILLIAM E. DAVIS, JR.

A BIRDER'S GUIDE TO NEW HAMPSHIRE. By Alan Delorey. American Birding Association, Inc., Colorado Springs, Colorado. 1996: 222 pp., 30 maps, 33 line drawings, 19 black-and-white photos. $16.95 (wire-o binding, wrap-around stiff paper cover).

A BIRDER'S GUIDE TO FLORIDA. By Bill Pranty. American Birding Association, Inc., Colorado Springs, Colorado. 1996: 388 pp., 83 maps, 29 line drawings. $18.95 (wire-o binding, wrap-around stiff paper cover).—These two recent additions to the American Birding Association's (ABA) birdfinding guide series, like the others in this series, are comprehensive birding guides, featuring excellent maps with text directions given to the nearest tenth of a mile. Both books have introductory sections which feature historical information on the region and cover topics such as weather, flora, birding hazards, birding ethics, and seasonal information. Both have numerous addresses and telephone numbers for local information, and both are graced with attractive line drawings. Both books have appendices with bar graphs illustrating status for each species by month, and the Florida guide has supplemental bar graphs showing status by region. The status codes are defined differently e.g., "rare but regular" (Florida) uses the same symbol as "Lucky to Find" (New Hampshire). Both contain faunal lists for animals other than birds (e.g., mammals, reptiles, butterflies), and both are well indexed both for bird species and location names.

The New Hampshire guide is divided into four regions with each region subdivided into local regions and loops, each with map and text. A chapter on the Bicknell's Thrush (*Ca-*

tharus bicknelli), recently promoted to species status, may be of particular interest to many. The Florida guide is divided into five regions, each extensively subdivided (e.g., 31 subdivisions for Central Florida), most with maps. A chapter on Florida specialty species, and a chapter listing exotic species may be of special interest.

Both books are "user friendly"—well-written, well edited, and well-illustrated. The books are sturdy and small enough (21.5 × 15 cm) to tuck into briefcase, glove compartment, or even a large pocket. I looked closely at the sections of each book which covered the areas of each state that I know best and found the coverage excellent. The wrap around rear cover irritates some people, but I find that it makes a good bookmark and offers protection for the book while traveling. I highly recommend both books to anyone with even a casual interest in birds and birding.—WILLIAM E. DAVIS, JR.

NORTH AMERICAN BIRD FOLKNAMES AND NAMES. By James Kedzie Sayre. Bottlebrush Press, Foster City, California. 1996: 291 pp. $24.95 (paper).—How many readers would recognize a bird called a "stone curlew" as a White Ibis (*Eudocimus albus*), a "water partridge" as a Green-winged Teal (*Anas crecca*), or a church martin as a European Starling (*Sturnus vulgaris*)? Hundreds of folknames and regional names have been applied to North American birds during the past four centuries, and Sayre has attempted to gather these names together into one book. A self-described amateur birder, Sayer traces his interest in bird folknames back to Neltje Blanchan's *Bird Neighbors* (Garden City Publishing, Garden City New York, [1898] 1925) which had a section entitled "also called" in the descriptions of many bird species. Sayre includes a bibliography of 63 references from which he compiled this book. The list contains the standard references (e.g., E. A. Choate and R. A. Paynter, Jr., "Dictionary of American Bird Names," Harvard Common Press, 1985; and E. S. Gruson, "Words for Birds" Quadrangle Books, New York, 1972) but is not exhaustive. For example, he does not list G. Trumbull's "Names and Portraits of Birds" (Haper & Brothers, New York, 1888) and hence is missing a few old or local names such as "duckinmallard" (duck and mallard) for the Mallard (*Anas platyrhynchos*) or "buzzard curlew" and "mowyer" (old word for one who mows) for the Long-billed Curlew (*Numenius americanus*). Thirty-four etymology references are also included which might be helpful to anyone wishing to delve into the subject on their own. Following a short introductory chapter, there is a chapter devoted to the origin of British bird names, since many were brought over to the New World with immigrants, and a chapter on the etymology of selected common North American bird names. This list includes mostly group names (e.g., warbler, vireo, oriole) but contains a number of individual species. Then follows a chapter on domestic birds including ornamentals, poultry, and cage and pet birds, and a sampling of birds seen in zoos, producing a rather odd assortment of etymologies. A brief chapter lists the more than 150 names for the flicker and contains a section describing the etymology of some of these names and their regional affiliation. The main section of the book (over 100 pages) then presents lists of names of each North American species listed by family in taxonomic order following the 1983 A.O.U Check-list (sixth ed.). The entries for each species consist largely of a list of names, with little reference to etymologies, regions, or references. The book is editorially naive. Latin names are italicized in some chapters but not in others, and although the A.O.U. Checklist is listed in the bibliography the common names do not consistently follow it. We do not really need to know that draft copies were printed on a Hewlett Packard Desk Writer at 300dpi. I found it an awkward statement that "The birds that reside in the Hawai'ian Islands have also been included, due to the islands long association with United States." A tighter editorial hand would have been most helpful. Despite its editorial short-

comings, the subject of the book is interesting and provides hundreds of names for North American species. The index, which runs nearly 80 pages, lists them all alphabetically. If you are interested in bird names and their origins, this book is one place to look for them.—WILLIAM E. DAVIS, JR.

STATUS, DISTRIBUTION AND BIOGEOGRAPHY OF THE BIRDS OF PARAGUAY. By Floyd E. Hayes, illus. by Dan Brown. American Birding Association, Inc., Colorado Springs, Colorado, 1995: 224 pp., 12 tables, 27 figs., color plates. $29.95 (paper).—This attractive and useful work is the inaugural monograph in a new series published by the American Birding Association. It is also the first overview of the Paraguayan avifauna in more than a half century.

The book contains the customary accounts of the geology of the country, its geography, vegetation, and climate, its ornithological history, and the author's field work. However, rather than the expected annotated list of the 645 species found in Paraguay, there is a slimmed-down coded checklist indicating for each bird its breeding or seasonal status, its habitat, and in which of the seven geographical regions it occurs.

Noteworthy distributional records, taxonomic problems, and species whose presences are hypothetical are each treated in separate chapters.

The chapter containing the biogeographical analysis is the scientific meat of the volume. Although Paraguay lacks topographic diversity, there are environmental gradients which are reflected in the composition of the vegetation and in that of the avifauna. Within this chapter are discussed the reasons for the regional differences in avian distribution, the barriers to dispersal, phenotypic variation, contact zones, etc.

A series of appendices give a complete chronological sequence of publications concerned with Paraguayan ornithology (of use to historians ?), a summary of the author's field work, the localities where western species reach their limits in eastern Paraguay and vice versa, a list of endangered species, and a gazetteer of ornithological localities.

The 27 figures, ranging from maps to color photos of habitats, are of outstanding quality.—RAYMOND A. PAYNTER. JR.

ECOLOGY AND EVOLUTION OF ACOUSTIC COMMUNICATION IN BIRDS. Edited by Donald E. Kroodsma and Edward H. Miller. Cornell University Press, Ithaca, New York. 1996:587 pp., black-and-white figs. $35.00 (paper); $75.00 (cloth).—A key resource for researchers in avian acoustic communication over the past 14 years has been Kroodsma and Miller's edited two volume set, "Acoustic Communication in Birds". The editors of that influential work have now introduced an update to this classic reference. Reflecting the growth in the field of avian bioacoustics, this volume has more numerous and, in many cases, more specialized chapters. Thirty-nine contributors have written 25 chapters and an appendix. These contributors are all leaders in their area of specialty and have written about what they have found most exciting in the field. However, one drawback of an edited volume is that there are a few notable omissions, both in terms of contributors and topics covered. Most notably, there is little coverage of the mechanisms of acoustic communication and only a single chapter on neural and endocrine factors. There is almost no coverage of syrinx anatomy or the physiological basis of sound production in birds. Although this book is focused on ecology and evolution, it is becoming more and more clear that ecologists need to consider proximate mechanisms. Similarly, neurobiologists and physiologists studying acoustic communication

in birds need to consider ecology and evolution more than they do. Unfortunately, this book is not integrative in this sense. It is an excellent reference for the topics that it does cover, and perhaps one of its only shortcomings is in the topics that it does not cover.

The book is very well organized. The chapters are organized into five sections: development, vocal repertoires, vocal variation in time and space, control and recognition of vocalizations, and the behavior of communicating. Each section has a brief introduction outlining and introducing the chapters within it. These sections are followed by an appendix on sound archives and instructions on how to best archive bird recordings. The literature cited in all chapters are compiled in a single references section, and each reference is cross-indexed to the pages on which it was cited. There are also both a subject and a taxonomic index. Thus, the book's organization facilitates its use as an excellent academic reference.

One theme running through the book is a call to tie research in avian acoustic communication to the conservation of avian species. One chapter is devoted to urging further study of bird sounds in the neotropics. One of the strengths in all of the chapters is in highlighting areas ripe for future study. I hope that this call to consider conservation will be heeded.

In the preface, the editors list three goals for this book. First, they wanted the book to be a showcase for the field of acoustic communication in birds. Second, they hoped the book will suggest areas rich for future research. Third, they hope the book will increase appreciation for species diversity and raise concern about conservation of species. The book should succeed on all three counts. In my reading, the book's most compelling success is in its second goal. This book will undoubtedly be a benchmark for the next decade in the study of the ecology and evolution of acoustic communication in birds.—SCOTT MACDOUGALL-SHACKLETON.

BLUEBIRDS FOREVER. By Connie Tops. Voyageur Press, Stillwater, Minnesota. 1994. 128 pp., 120+ color photos. $22.95 (paper).—The many energetic supporters of bluebirds have built and placed more than 500,000 nest boxes along the roadways of North America. These boxes have been instrumental in the remarkable comeback of declining bluebird populations and appear to have caused an increase in their range. The present book documents that effect, the people who participate in it, and ways that the reader can participate in the work. Through accounts of the efforts of local bluebird fans at widely scattered sites across the United States, the author elaborates on what must be done to encourage bluebirds. It truly is remarkable that some groups have built 500–2000 boxes over a weekly session in this effort. (Or is it more remarkable that one group of volunteers built a bluebird trail of more than 3000 boxes that completely spans the length of Montana at an interval of more than 3 boxes/km!).

Predator control, discouraging pests, nest-box design, placement of nest boxes, and numerous other topics are discussed. If you love bluebirds, you'll love this book. If you don't think much of bluebirds, one way or the other, after you read this book you'll love them. The beauty of the color photos is well worth the price of the book. Add to that the readable, easy prose and you have a very fine publication. The author provides plans for several kinds of successful bluebird nest boxes and cites much of the relevant published literature regarding bluebird biology.—C. R. BLEM

Wilson Bull., 109(4), 1997, pp. 762–778

PROCEEDINGS OF THE SEVENTY-EIGHTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The seventy-eighth annual meeting of the Wilson Ornithological Society was held Thursday, 17 April, through Sunday, 20 April, 1997, at Kansas State University, Manhattan, Kansas, in joint session with the Kansas Ornithological Society. The local committee, chaired by John Zimmerman, was composed of George Allen, Doris Burnett, Ted Cable, Jack Cully, Jim Mayhew, Dan Mulhern, Chuck and Jane Otte, Diane Post, Dave Rintoul, Bob Robel, Chris Smith, and Marilyn Tilghman. The meeting was sponsored by the Division of Biology, Kansas State University; the Graduate School, Kansas State University; the Northern Flint Hills Audubon Society; the Friends of Konza Prairie; the Kansas Department of Wildlife and Parks; the Kansas Cooperative Fish and Wildlife Research Unit; and the Kansas Chapter of the Wildlife Society.

The Council met from 13:09 to 18:08 on Thursday, 17 April, in the K-State Student Union. At that time there were 163 registrants. On Thursday evening there was an informal reception for conferees and their guests at the Beach Museum of Art.

The opening session on Friday convened in Forum Hall at 08:30 with welcoming remarks from Provost James Coffman, Kansas State University, followed by responses from President Keith Bildstein, Wilson Ornithological Society, and President Roy Beckmeyer, Kansas Ornithological Society, with further comments from local committee chair John Zimmerman and scientific program committee chair, WOS Second Vice-president John Kricher. Following these opening remarks, WOS First Vice-president Edward H. Burtt, Jr., introduced the first annual Margaret Morse Nice Plenary Lecture, "Seeking to Understand the Living Bird," presented by Nicholas and Elsie Collias. This informative and delightful presentation was very well received. The Nice Lecture was followed by the first business meeting of the Wilson Ornithological Society.

The scientific program included 89 contributed papers and 15 contributed posters, which were organized into 11 paper sessions, a poster session, a symposium on the ornithology of wrens organized by Greg Farley and Dale Kennedy, a second symposium on the ornithology of the Great Plains organized by John Kricher and John Zimmerman, a third symposium on Great Plains Grassland Birds and the Conservation Reserve Program organized by Robert Robel, a workshop on state and regional ornithology journals organized by Albert R. Buckelew, Jr., and a second workshop on teaching ornithology organized by Edward H. Burtt, Jr.

On Friday evening the conferees enjoyed a picnic on the Konza, a 3487-ha tallgrass prairie owned by The Nature Conservancy and managed for ecological studies by the Division of Biology at Kansas State University. Field trips on Friday, Saturday, and Sunday mornings included jaunts to Milford Reservoir, Tuttle Creek Reservoir, and to the Konza Prairie to observe lekking prairie chickens. On Sunday there was an all-day field trip to Cheyenne Bottoms/Quivira National Wildlife Refuge.

A social hour preceded the annual banquet, which was held in the Main Ballroom of the K-State Student Union. At the conclusion of the enjoyable dinner President Bildstein briefly addressed the conferees, and the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 108 of *The Wilson Bulletin*)

Larry Clark, "Trigeminal repellents do not promote conditioned odor avoidance in European Starlings." Wilson Bull. 108:36–52.

LOUIS AGASSIZ FUERTES AWARD

Erik D. Doerr, "The population genetic consequences of natal philopatry in birds."

MARGARET MORSE NICE AWARD

Ann (Sandy) Kownacki, "An investigation into mass die-offs of flamingos at Lake Nakuru, Kenya."

PAUL A. STEWART AWARDS

Eric C. Atkinson, "Mass differences between vernally and autumnally migrating Northern Saw-whet Owls (*Aegolius acadicus*) in southeast Pennsylvania."

Emilio M. Bruna, "Effect of habitat fragmentation on tropical plant-pollinator interactions."

Daniel A. Cristol, "Are 'Carolina' juncos really short-distance migrants?"

James R. Miller, "Avian diversity and predator assemblages along a gradient of urbanization."

Kelley Segars, "Comparison of bird communities in developed and undeveloped riparian areas."

WILSON ORNITHOLOGICAL SOCIETY TRAVEL AWARDS

Sara R. Dewey, "Effects of food availability on parental care strategies and juvenile survival in Northern Goshawks."

Oliver Komar, "Estimating detection probability for temperate forest birds in winter."

James R. Miller, "Nest predation in riparian areas along the Colorado Front Range: the effect of urbanization."

ALEXANDER WILSON PRIZE (for best student paper)

James R. Miller, "Nest predation in riparian areas along the Colorado Front Range: the effect of urbanization."

Selection committee for the Edwards Prize—Charles Blem (chair), Robert Beason, Mary Clench, James Sedgewick, and Richard Stiehl; for the Fuertes, Nice, and Stewart Awards—Daniel Klem, Jr. (chair), Judith M. Rhymer, and Richard Stiehl; for the Wilson Ornithological Society Travel Award—John C. Kricher (chair), Edward H. Burtt, Jr., and William E. Davis, Jr.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Bildstein at 10:03 on Friday, 18 April, in Forum Hall. Secretary Smallwood then summarized what had transpired at Thursday's council meeting, noting the successful efforts of John Zimmerman and the local committee and of Second Vice-president John Kricher and the scientific program committee. He reviewed the awards offered by the Society, the winners to be announced at the annual banquet. Secretary Smallwood invited those in attendance to visit the WOS home page on the internet, and to forward any suggestions and complements to webmeister Janet Hinshaw. He noted that the *Ornithological Newsletter* is now posted on the internet, as well. The secretary introduced the newly elected editor of *The Wilson Bulletin*, Bob Beason, who hails from the State University of New York at Geneseo. Editor Beason will institute some changes to the *Bulletin's* format, including an increase in the journal's size to 8 × 10 inches,

and adoption of a two-column layout. He will encourage e-mail communication among authors, reviewers, and the editorial office, and will seek to receive final manuscript submissions on disk. Those in attendance welcomed the new editor, and commended retiring Editor Charlie Blem and Assistant Editor Leann Blem for a remarkable 10 years of dedicated service to the Wilson Ornithological Society. Secretary Smallwood then noted that membership in the Society currently stood at 2512, including 328 student and 517 life members, and that the Society has been enjoying a modest increase during the past few years. The 1998 annual meeting will be held 6–12 April in St. Louis, in joint session with the American Ornithologists' Union, the Association of Field Ornithologists, the Colonial Waterbird Society, the Cooper Ornithological Society, and the Raptor Research Foundation. This meeting will be known as the Second North American Ornithological Conference. First Vice-president Burtt will gratefully entertain suggestions for the second annual Margaret Morse Nice Plenary Lecture. Due to a change in plans, the 1999 WOS meeting will not be held at the University of North Carolina in Greensboro, and Council was exploring options for alternate venues. President Bildstein appointed Dick Conner to chair the reconstituted resolutions committee. The secretary then asked those assembled to stand in recognition of the following WOS members who had passed away since we last met: Richard A. Anderson (St. Louis, MO), William B. Davis (Bryan, TX), Phillip A. Dumont (Flagler Beach, FL), Roger Tory Peterson (Old Lyme, CT), Allen R. Phillips (Nuevo Leon, Mexico), and Carol S. Roesler (Darien, CT).

The treasurer's report was then presented by Doris Watt.

Charles Blem offered the editor's report.

Jerome A. Jackson, chair, delivered the report of the nominating committee, which also included Mary H. Clench and Richard N. Conner, offering the following slate of candidates: President, Edward H. Burtt, Jr.; First Vice-president, John C. Kricher; Second Vice-president, William E. Davis, Jr.; Secretary, John A. Smallwood; Treasurer, Doris J. Watt; and Members of Council for 1998–2000, Charles Blem and Sara R. Morris.

The first business meeting was adjourned at 10:21.

SECOND BUSINESS MEETING

The second business meeting was called to order by President Bildstein at 13:05, Saturday, 19 April, in Forum Hall, at which time he asked Secretary Smallwood to read aloud two resolutions to be considered:

COMMENDATION

WHEREAS the Wilson Ornithological Society and the Kansas Ornithological Society held a joint meeting in Manhattan, Kansas, at the invitation of the Division of Biology and the Graduate School, Kansas State University, the Northern Flint Hills Audubon Society, the Friends of the Konza Prairie, the Kansas Department of Wildlife and Parks, the Kansas Cooperative Fish and Wildlife Research Unit, and the Kansas Chapter of the Wildlife Society; and

RECOGNIZING that the Committee on the Scientific Program, directed by John C. Kricher, coordinated a remarkable program of contributed papers, including several workshops and symposia, as well as poster presentations; and

RECOGNIZING that the Committee on Local Arrangements, under the able direction of John L. Zimmerman, provided an outstanding conference venue which exemplified the habitats, wildlife, ambiance, and hospitality indigenous to the Great Plains; and

WHEREAS having been some time in preparation a splendid time was guaranteed for all,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commend the Committee on the Scientific Program, the Committee on Local Arrangements, and our Kansan sponsors for a most successful and enjoyable meeting in Manhattan.

The motion to accept this resolution was made by John Kricher and seconded by Herb Hendrickson, and it passed by acclamation.

COMMENDATION

WHEREAS Charles R. Blem has served the Wilson Ornithological Society in the capacity of editor of *The Wilson Bulletin* for the past ten years; and

WHEREAS though his editorial skills and leadership he has enhanced the international reputation of *The Wilson Bulletin* as one of the most prestigious journals of ornithology; and

WHEREAS through his faithful and relentless efforts, and those of his dedicated editorial staff, especially those of his partner, Assistant Editor Leann Blem, the Wilson Ornithological Society has consistently produced a world-class publication, delivered on schedule;

THEREFORE BE IT RESOLVED that the Officers, Council, and Membership of the Wilson Ornithological Society express their deepest appreciation to Editor Blem and his associates for their many years of commitment and service to their Society.

The motion to accept this resolution was made by Ted Davis and seconded by John Kricher. The resolution was enthusiastically passed by the membership, who rose to offer Editor Charles Blem and Assistant Editor Leann Blem a heartfelt standing ovation.

President Bildstein recalled the report of the nominating committee to the floor. Jerome A. Jackson, chair, solicited additional nominations from those assembled. As there were none, Herb Hendrickson moved and Joseph Jehl seconded that the nominations be closed, and further, that the secretary cast a unanimous ballot for all offices. The motion passed by acclamation and the secretary did as directed.

Kim Smith next addressed the assembly with an update on the 1998 North American Ornithological Conference in St. Louis. Bette Loiselle and Jeffrey Brawn will chair the local and scientific program committees, respectively. An evening reception is planned for Tuesday, 7 April, and the following day the scientific program will commence with the second annual Margaret Morse Nice Plenary Lecture.

President Bildstein distributed a "get-well" card so that the attendees could send their best wishes to Olin Pettingill, who was recovering from an illness. Calling for additional announcements and receiving none, the president then received a motion from John Kricher, seconded by Jerome Jackson, that the meeting be adjourned. Those assembled in agreement, adjournment occurred at 13:30.

REPORT OF THE TREASURER
1 July 1996 to 30 June 1997

GENERAL FUNDS

Balance Forward		$ 68,164.22
Receipts		
Regular and Sustaining Memberships	$ 33,413.00	
Student Memberships	5,030.00	
Family Memberships	198.00	
Total Dues		$ 38,641.00

Subscriptions	$ 25,760.00	
Newsletter	337.28	
Back Issues	388.00	
Page Charges	18,190.00	
Total Income from Publications		$ 44,675.28
Contributions: Research Fund	$ 269.00	
Van Tyne Library	2,870.00	
General Endowment	107.00	
Life, Patrons (Gen Endowment)	2,000.00	
WOS Student Travel Fund	806.00	
Unrestricted	3,132.00	
Total Contributions		$ 9,184.00
Royalties		1,755.00
Interest from Endowments		24,608.52
Dividends from Dreyfus Acct (reinvested)		(957.53)
		28,458.40
Miscellaneous		
Net OSNA Adjustment		−69.90
TOTAL RECEIPTS		$120,888.78
Disbursements		
Bulletin Publication		
June 1996	$ 17,587.51	
September 1996	19,932.75	
December 1996	23,274.49	
March 1997		
Editor's expenses	5,000.00	
Total Publication Costs		$ 65,794.75
OSNA Expenses	$ 18,258.83	
Secretary's expenses	68.00	
Treasurer's expenses	69.57	
Treasurer's bond		
CPA (tax filing and audit)	1,600.00	
Incorporation Fee	5.00	
Editor's honorarium	2,000.00	
Editor's travel	506.36	
Postage	74.30	
Awards Committee phone	13.06	
Van Tyne Library (back issues)	200.00	
Advertisement (Allen Press)		
Meeting costs (speaker airfare)	321.00	
Miscellaneous	185.40	
Total Operating Expenses		$ 23,301.52
Organizational Awards	$ 2,899.99	
Ornithological Council Contribution	1,880.00	
ABC Dues	150.00	
Total Philanthropies		$ 4,929.99
TOTAL DISBURSEMENTS		$ 94,026.26
Ending Balance		$ 95,026.74

CASH ACCOUNTS

First Source Bank Checking 30 June 1997	$ 74,408.46	
Dryfus Liquid Assets 30 June 1997	20,618.28	
Total Cash on Hand		$ 95,026.74
Van Tyne Library Accounts Starting Balance	$ 3,955.41	
Receipts	$ 1,181.52	
Expenses	2,035.95	
Ending Balance		$ 3,100.98

SUTTON DESIGNATED ACCOUNTS

Endowment Principal as of 1 July 95	$ 55,747.58
Increase in Principal Value June 95–96*	65,503.41
1996 Earnings**	2,489.13
Funds disbursed for Color Plates (2)	1,635.00
Balance	854.13

TOTAL ENDOWMENT FUNDS

1996 Market Value	$676,029.00
1997 Market Value	$814,315.00

* 17.5%

** Based on 3.8% interest on Mellon account

EDITOR'S REPORT—1996

In 1996, 200 manuscripts (96 major papers, 104 short communications) were received by *The Wilson Bulletin* editorial office. This is 18 less than in 1995, but well over the average of the past decade (about 175/year). Of these, approximately 64% were rejected. The time between receipt of manuscript from the author(s) and our return of the manuscript with referee comments nearly always has been less than three months. A few manuscripts required slightly more than four months for a decision. The average time between receipt of a manuscript and its appearance in *The Wilson Bulletin* in 1996 was almost always less than a year, as in past issues. We are using email in the editorial process to the degree that some costs have been reduced and the speed of response for computer users often is more prompt.

I am grateful to the editorial board—Kathy G. Beal, R. N. Conner, Tom Haggerty, and J. A. Smallwood—for their timely, skilled evaluations of many of the manuscripts submitted to the journal. Assistant Editors Leann Blem and Albert E. Conway are responsible for the consistency of style and format, and for making arcane prose more readable. I thank them for their efforts. Kathy G. Beal deserves special praise for continuing to assemble the index for *The Wilson Bulletin*. This a tedious task and the entire society benefits from her careful work. Leann Blem has provided much of the manual labor that keeps the editorial office running and she catches many of the small errors that can plague a publication. Virginia Commonwealth University Department of Biology supports the editorial process and the running of the office in numerous ways. As always, I remain open to suggestions as to how to improve the service we provide the readers and authors, and invite you to make your opinions known to me.

C. R. Blem, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

The current members of the WOS membership committee are Jim Ingold at Louisiana State University, Mark Woodrey at the Mississippi Museum of Natural Science, Mary Clench of Gainesville, Florida, Laurie Goodrich at Hawk Mountain Sanctuary, and myself, at Montclair State University in New Jersey.

Laurie Goodrich has been overseeing the WOS membership poster's travel itinerary. This past year the poster was displayed at the WOS meeting in Cape May, New Jersey; the meeting of the Pennsylvania Chapter of the Wildlife Society; the Pennsylvania Society for Ornithology meeting; the American Birding Association meeting in Salt Lake City; and the joint American Ornithologists' Union and Raptor Research Foundation meeting in Boise, Idaho. Although the poster did not find a passage to the Association of Field Ornithologists meeting, the WOS brochures did arrive safely.

Mary Clench will be contacting nonrenewing members to invite them back into our flock. Mark Woodrey continues to send membership invitations to authors who publish in *The Wilson Bulletin,* and Jim Ingold contacts nonmembers who make presentations at the annual meetings.

Last year I received about a dozen letters from people interested in joining us. To each I sent a letter of welcome and our membership brochure. I also respond to periodic requests from Richard Walker, business manager at Allen Press, for replenished supplies of our membership brochure.

John A. Smallwood, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

Introduction

The mission of the Committee on Undergraduate Outreach, which was established in June, 1991, is to stimulate an interest in ornithology among undergraduate students, and to help to maintain and focus that interest so as to stimulate students to continue studies in ornithology. The Committee explores ways to increase interest of undergraduate students in ornithology both as a focus for future postgraduate studies, and as an avocation for those who seek careers in fields other than the biological sciences.

Members of the Committee during 1996–97 are (alphabetically): Albert R. (Jay) Buckelew, Jr., Department of Biology, Bethany College, Bethany, WV; Edward H. Burtt, Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH; Dale Kennedy, Biology Department, Albion College, Albion, MI; Lynn A. Mahaffy, Randolph-Macon College, Ashland, VA; Barnaby Marsh, IV, Cambridge, MA; Dan A. Tallman, Mathematics and Natural Sciences, Northern State University, Aberdeen, SD; Ernest J. Willoughby, Department of Biology, St. Mary's College of Maryland, St. Mary's City, MD; W. Herbert Wilson, Department of Biology, Colby College, Waterville, ME.

Activities

1. The Committee's Guide to Graduate Programs in Ornithology is getting final corrections at this moment, and we have discussed with Janet Hinshaw of the Library Committee the possibility of posting the document on the WOS Internet web page. This can be accomplished very soon. We think this would be the most cost-effective way to distribute the document to interested persons, pending an arrangement to print and sell copies to those

who want it in that form. Dale Kennedy and Ernie Willoughby have done most of the work on this project.

2. Report on the survey of undergraduate ornithology courses in North America. This project was spearheaded by Jed Burtt and Herb Wilson in 1993, and presented as part of the Symposium on Undergraduate Outreach at the meeting in Guelph, ON. Drs. Burtt and Wilson have prepared a manuscript summarizing the information and have submitted it to *Wilson Bulletin* to be considered for publication.

3. The Committee is preparing a guide to Federal regulations governing the collecting and holding of bird specimens for teaching purposes, as a resource for instructors in undergraduate institutions. Jay Buckelew is leading this project, and is making progress untangling the regulations, which appear to be in flux.

4. We continue to discuss the project to develop video-taped interviews with eminent ornithologists, to be lent through the WOS Library, as a resource to inform and inspire potential ornithologists. Dale Kennedy and Lynn Mahaffy have developed standard interview questions, based on their surveys on what undergraduate students would most likely want to know about these scientists, and Dr. Mahaffy is looking into the question of the kind of legal release form that would have to be signed in order to distribute such interviews through the lending library without legal entanglements.

5. Jed Burtt and John Kricher organized a Workshop on Undergraduate Teaching in Ornithology for the 1996 Annual Meeting, and Dr. Burtt has done so again for the 1997 meeting. This symposium is scheduled for Saturday Morning, April 19, with seven persons participating. The papers contributed in these workshops may eventually appear as a laboratory manual.

Ernest J. Willoughby, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Each year it becomes newly apparent, to this (only peripherally involved) chairman, how much really goes on in our segment of the WOS. The activity takes place primarily in the library of the UMMZ Bird Division; but it comprises interaction with the membership at large, with the Society treasurer, with the publisher and distribution facilities—and with a whole national and worldwide complex of other agencies and other scientific organizations.

The mere keeping and assembling of the records has become a major ongoing task. In that connection, the Committee is strongly committed to continuing a calendar-year timeframe for reporting on *our* various activities. If some of the figures seem a little on the downside from last year (calendar 1995), it is in part due to mere irregularities in recording and compiling information. The computer, of course, is a big help these days in having things organized.

That we continue at all to keep everything moving, and the records in respectable order, is still owing to the constant efforts of Janet Hinshaw and her helpers, who give unstintingly of their time here in the Bird Division. Special thanks go to the new Bird Division Secretary, Maricel Fuentes, who handles most of the library loans and xeroxing. Suffice it to say once more, that everything is still progressing nicely, as the figures below should demonstrate.

To itemize, as succinctly as possible:

Donations received—19 books, 676 journal issues, 1 thesis, 15 reports, 1 tape, and 445 reprints, from the following 24 donors: R. Banks, R. Bayer, K. Bildstein, C. Blem, C. Braun, E. Brinkley, D. Chetkovich, G. Christensen, J. Greenlaw, G. Hall, K. Haller, J. Hinshaw, R. Hoffman, L. Kiff (for The Peregrine Fund), J. Marshall, F. Lohrer (for OSNA), W. Post, J. R. Schrock, G. A. Smith, J. Tate, Washington Ornith. Soc., E. O. Willis, R. Whiting, and H. Zernickow.

Library Loans—87 loan transactions to 27 people included 244 items and photocopies.

Publications regularly received, including exchanges—a total of 227 titles from 183 organizations included exchanges of 158 journals and reprints from 128 organizations, 38 titles as gifts from 31 individuals and organizations, and 31 titles as subscriptions from 24 organizations.

Gifts to other institutions—Carnegie Museum of Natural History (3 journal issues), Museum A. Koenig, Germany (1 journal issue), and Univ. Estadual Paulista, Brazil (205 journal issues).

Trades with other institutions—North Carolina State Museum (we sent 8 books in return for 17 books and 22 journal issues), Emil Urban/Birds of Africa (sent 71 journal issues; will receive 1 vol. of Birds of Africa), and The Peregrine Fund (we received 9 books and 1 journal issue; exchange material yet to be decided).

Books sold, and New Book Fund—41 books and 5 journal issues were sold for $1978.91, $600 in credit from Buteo Books, and $1978.91 which was added to the New Book Fund.

Library Purchases—Included 39 books, 1 thesis, and 381 journal issues, for a total of $2209.11, including $1195.11 cash and $1014.00 from our credit with Buteo Books.

We would like to remind everyone of our web page which can be found at http://www.ummz.lsa.umich.edu/birds/wos.html. We have recently added a list of our currently received serials and information on requesting items from the library.

In closing: again, thanks to all our members for their continuing help, and for their active use of our facility. May this continue and expand in the years to come.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The following is submitted as a brief report of activities of the Conservation Committee of the Wilson Ornithological Society during 1996–97.

During the past year we have been working on projects in three problem areas:

1. The role and status of birds in riverine ecosystems.
2. The issuance and use of bird depredation permits.
3. The Endangered Species Act and problems associated with its implementation and reauthorization.

I will summarize these in the order presented.

1. Riverine ecosystems have been altered dramatically over the past five centuries, and although considerable attention has been given to such problems as channelization and dam construction, the focus of most attention has been on alteration of the aquatic environment and the ways in which such alteration affects aquatic organisms. We have been looking at the influences of such alteration on birds, including aquatic, littoral, and bottomland forest species. Specifically we have been documenting and summarizing the diverse ways in which birds have been and are being affected. As examples of the range of influences of riverine ecosystem changes on birds, we cite the loss of nesting habitat for sandbar nesting species such as the Interior Least Tern by dredging and channelization, the alteration of the avian piscivore prey base as a result of release of cool, clear bottom water from behind dams on the Colorado River and the introduction of Rainbow Trout, and the probable alteration of bird species as a result of changing the composition of bottomland hardwood forests through alteration of flooding frequencies.

2. Bird depredation permits are issued throughout North America to "alleviate" "perceived problems" in aquaculture, agriculture, and urban/suburban environments. These range from permits issued to kill or harass cormorants at catfish ponds in Mississippi to

permits issued to kill or harass vultures in Virginia. We are trying to document (a) the geographic and taxonomic range of permits being issued, (b) the nature and extent of knowledge of the validity of the problems for which permits are issued, and (c) the nature of implementation of these permits and the nature of monitoring of implementation.

3. The Endangered Species Act of 1973 is probably the most important piece of environmental legislation ever passed. Unfortunately its implementation varies considerably and there are strong forces opposing the reauthorization of such a strong Act. Several modifications have already been made to the Act, some of which improve it, others which weaken it. One modification was the provision for issuance of "incidental take" permits to private landowners if they present an acceptable Habitat Conservation Plan. Such Habitat Conservation Plans have come under considerable and continuing scrutiny. Some, for example, call for the removal of a species to public land to allow destruction of the habitat on private land. As a result, species populations are becoming increasing fragmented and increasingly dependent on public lands. Some plans deal with multiple species. Statewide Habitat Conservation Plans and Safe Harbor approaches are now being developed. These relinquish the Endangered Species Act authority to the individual states. Some, such as ones known as "Safe Harbor" provide the landowner with a 99-year exemption from the provisions of the Endangered Species Act. "Safe Harbor," incidentally, does not refer to a safe place for the species — it refers to the safety of the landowner from the teeth of the Endangered Species Act. Such plans are in association with a current administration theme known as "No Surprises." "No Surprises," like "Safe Harbor" is intended to give land owners assurance that once they do what mitigation is required by their Habitat Conservation Plan, they have no further obligations. These programs ignore the complexity and change inherent in natural ecosystems.

Unfortunately, the environmental community is very divided on the private lands issue. The Environmental Defense Fund strongly favors Habitat Conservation Plans and Safe Harbor approaches. Other groups such as National Audubon, National Wildlife Federation, Sierra Club Legal Defense Fund are opposing them. It is very important at this point that we as ornithologists very carefully scrutinize the available information on these programs and that we not just "sign on."

For the past year I have been working on these Endangered Species Act issues and last year I had the opportunity to meet with White House officials and Congressional leaders concerning them. I also spoke about them at a National Audubon Convention in Washington and will be speaking about them at a National Wildlife Federation conference next month. The important words at this time are "caution" and "understanding." We do not want to compromise away the future for endangered species. Are mitigation approaches, Habitat Conservation Plans, Safe Harbor, and other approaches helping species or are they simply allowing "business as usual"? We need to be involved.

Jerome A. Jackson, *Chair*

The Committee on the Scientific Program, chaired by John C. Kricher, with Edward H. Burtt, Jr., and William E. Davis, presented the following program assisted by session moderators and symposium and workshop organizers James C. Bednarz, Kimberly S. Bostwick, Albert R. Buckelew, Jr., Edward H. Burtt, Jr., Jack F. Cully, Jr., William E. Davis, Jr., Greg H. Farley, Danny J. Ingold, E. Dale Kennedy, John C. Kricher, James R. Miller, Helmut C. Mueller, K. Otter, Robert J. Robel, Eric R. Stone, David L. Swanson, and John L. Zimmerman.

PAPER SESSIONS

J. F. Cully, Jr., and H. L. Michaels, Kansas State Univ., Manhattan, KS, "Avian diversity and the Intermediate Disturbance Hypothesis at Fort Riley Army Reserve, Kansas."

J. W. Walk and R. E. Warner, Univ. of Illinois, Urbana, IL, "Influence of management and patch size on the distribution of grassland birds."

T. H. Parker, Kansas State Univ., Manhattan, KS, "Segregation of nest sites and relationship to predation on the prairie."

D. E. Hoover, Kansas State Univ., Manhattan, KS, "Avian composition and relative abundance in fenced and grazed riparian habitats in southeastern Kansas."

D. J. Ingold, Muskingum College, New Concord, OH, "The influence of nest boxes on Northern Flicker reproductive success in the presence of European Starlings."

R. N. Conner and C. E. Shackelford, Southern Research Station, Nacogdoches, TX, "A multivariate evaluation of woodpecker-habitat associations in eastern Texas forests."

D. C. Rudolph, R. N. Conner, and S. J. Burgdorf, Southern Research Station, Nacogdoches, TX, "The consequences of Red-cockaded Woodpecker management on rare species of the west Gulf coastal plain."

D. Sasnz and R. N. Conner, Southern Research Station, Nacogdoches, TX, "Pileated Woodpecker damage to Red-cockaded cavity trees in eastern Texas."

J. A. Grzybowski, Univ. of Central Oklahoma, Edmond, OK, and C. M. Pease, Univ. of Texas, Austin, TX, "Abandoning parasitized nests: benefits and costs to seasonal fecundity."

M. E. Baltz, Univ. of Missouri, Columbia, MO, "Rejection of artificial parasite eggs by a naive avian host."

D. K. Beutler, Washington State Univ., Pullman, WA, "Brown-headed Cowbirds in forested landscapes: local and landscape factors."

P. F. Elliott, Eastern Connecticut State Univ., Willimantic, CT, "Demographic implications of cowbird depredation of songbird nestlings."

R. O. Prum, Univ. of Kansas, Lawrence, KS, "Phylogenetic interrelationships of the cotingas (Cotingidae) based on morphology and DNA."

N. Rice, Univ. of Kansas, Lawrence, KS, "Phylogeny of the Formicariidae."

K. Zyskowski and R. O. Prum, Univ. of Kansas, Lawrence, KS, "Phylogenetic analysis of nest architecture of the neotropical ovenbirds (Furnariidae)."

J. A. Stratford, Southeastern Louisiana Univ., Hammond, LA, "The role of vegetation structure in the local distribution of terrestrial insectivores in a fragmented neotropical landscape."

D. P. Craig, Univ. of Colorado, Boulder, CO, and M. C. Yaber, Purdue Univ., Layfayette, IN, "Patterns of nest predation by clutch size, nest placement, and successional stage in a Costa Rican rainforest."

K. S. Bostwick and R. O. Prum, Univ. of Kansas, Lawrence, KS, "Mechanical sound production in *Machaeropterus* (Pipridae)."

K. J. McKay, Midwest Raptor Research Fund, Moline, IL, and P. C. Petersen, Quad City Audubon Society, Davenport, IA, "Midwestern raptor population trends as determined by forty years of Christmas Bird Count data."

K. J. McKay, Midwest Raptor Research Fund, Moline, IL, and P. C. Petersen, Quad City Audubon Society, Davenport, IA, "Using Christmas Bird Count data to monitor populations of Icterids and species associated with humans."

M. B. Robbins and D. Mead, Univ. of Kansas, Lawrence, KS, "Population trends in riparian birds: an improved census method."

O. Komar, Ohio Wesleyan Univ., Delaware, OH, "Estimating detection probability for temperate forest birds in winter."

J. C. Bednarz, Arkansas State Univ., State University, AR, D. M. Evans, PNW Experiment Station, Olympia, WA, and J. C. Hovis, Arkansas State Univ., State University, AR, "A validation test of point-count techniques for estimating breeding bird abundance."

J. R. Jehl, Jr., Hubbs-Sea World Research Institute, San Diego, CA, "Monitoring Wilson's Phalaropes: lessons from 17 years of trying."

A. R. Buckelew, Jr., Bethany College, Bethany, WV, "The role of state and regional journals in contemporary ornithology."

J. A. Jackson, Mississippi State Univ., Mississippi State, MS, "The origins and journeys of state and provincial bird journals."

W. E. Davis, Jr., Boston University, Boston, MA, "Strategies for the production of a successful local bird journal: a case study."

C. R. Mauk, Univ. of Kansas, Lawrence, KS, "A phylogenetic analysis of display behaviors of grebes (Aves: Podicipedidae)."

H. Ewell, Univ. of Colorado, Boulder, CO, "Foraging behavior of the Pygmy Nuthatch (*Sitta pygmaea*) in ponderosa pine forests."

R. C. Beason, State Univ. of New York, Geneseo, NY, "Evidence for multiple magnetic receptors in the Bobolink."

H. G. Gamer and J. C. Bednarz, Arkansas State Univ., State University, AR, "Dynamics and stability of a population of wintering Red-tailed Hawks in the delta region of Arkansas."

V. B. Estelle and S. D. Earsom, Colorado Bird Observatory, Brighton, CO, "Observations of Mountain Plover staging in southeastern Colorado and wintering in Mexico."

H. C. Mueller, Univ. of North Carolina, Chapel Hill, NC, "Age and sex differences in timing of migration of hawks."

K. Highfill and Student Research Team, Lawrence High School, Lawrence, KS, "Remote videotaping of Great Horned Owls (*Bubo virginianus*) nesting in a flower pot."

M. C. Brittingham, G. R. Wilson, Pennsylvania State Univ., University Park, PA, and L. J. Goodrich, Hawk Mountain Sanctuary Association, Kempton, PA, "How well do artificial nests estimate success of real nests?"

K. K. Wenger, Ohio Wesleyan Univ., Delaware, OH, "The avian ecology of Actinomycetes: another feather-degrading bacterium."

D. M. Watson, Univ. of Kansas, Lawrence, KS, "Mistletoe: a key determinant of bird diversity in Australian woodlands."

T. K. Nakamura, Univ. of Colorado, Boulder, CO, "Recent introduction and expansion of the House Sparrow (*Passer domesticus*) in Puerto Rico."

L. G. Ball, Univ. of Kansas, Lawrence, KS, "Conservation strategies for the birds of the Philippines."

K. Otter, L. Ratcliffe, D. Michaud, and P. T. Boag, Queens Univ., Kingston, ON, Canada, "Do female Black-capped Chickadees prefer high ranking males as extra-pair partners?"

M. T. Gaudette and R. P. Brooks, Pennsylvania State Univ., University Park, PA, "Prediction of wetland songbird community integrity for cumulative impact assessment."

G. Farley, Fort Hays State Univ., Hays, KS, "A possible function for ancillary nest building in wrens."

J. F. Cavitt, Kansas State Univ., Manhattan, KS, "Patterns of mass loss in breeding House Wrens: are parents stressed?"

N. S. Dubois, Albion College, Albion, MI, "Bewicks Wrens respond more aggressively to song of House Wrens than to conspecific song."

J. Walsh and C. E. Bock, Univ. of Colorado, Boulder, CO, "Likely occurrence of overlapping broods in the Rock Wren."

D. W. White and E. D. Kennedy, Albion College, Albion, MI, "Effect of habitat on nest destruction by House Wrens."

D. Marija, St. Petersburg Univ., St. Petersburg, Russia, "Ecology and behavior of the Wren *Troglodytes t. troglodytes* in the Leningrad region (Russia)."

J. Gubanyi and J. Savidge, Univ. of Nebraska, Lincoln, NE, "Stopover ecology of spring migrants along the Missouri and Platte rivers in eastern Nebraska."

K. L. Dean, D. L. Swanson, and E. T. Liknes. Univ. of South Dakota, Vermillion, SD, "Age structure and phenology of neotropical woodland migrants in the northern Great Plains during fall migration."

C. R. Davis, Arkansas State Univ., State University, AR, "Habitat and landscape use by selected neotropical migratory birds in the coniferous forests of Idaho."

E. T. Liknes, Univ. of South Dakota, Vermillion, SD, "Neotropical migrant flight ranges and migratory patterns from southeastern South Dakota: are the northern Great Plains a barrier to migration?"

D. A. Kluza, Univ. of Kansas, Lawrence, KS, "Causation of population declines in neotropical migrant birds."

J. C. Gering, Miami Univ., Oxford, OH, "Characterization of overwintering and breeding bird communities of two subtropical habitats—Bahama pine forest and dry evergreen forest."

K. J. McKay, J. W. Stravers, B. R. Conklin, U. Konig, and S. Hawks, Midwest Raptor Research Fund, Moline, IL, "Assessment of human activity impacts on Bald Eagle reproductive success along the upper Mississippi River."

J. M. Schukman, Leavenworth, KS, "Interspecific association of area-sensitive forest birds in eastern Kansas."

J. G. Hallett, D. K. Beutler, Washington State Univ., Pullman, WA, and M. A. O'Connell, Eastern Washington Univ., Cheney, WA, "Avian communities of managed forests of northeastern Washington: habitat relationships."

J. F. Chace, Univ. of Colorado, Boulder, CO, "Solitary Vireos nesting in a fragmented landscape: the effect of nest parasitism and predation on population growth."

J. C. Hovis, Arkansas State Univ., State University, AR, "Survival and site fidelity of Swainson's Thrushes related to landscape patterns."

J. M. Ruth, USGS, Fort Collins, CO, "Effects of surrounding land uses on avian communities."

J. Miller, Colorado State Univ., Fort Collins, CO, "Nest predation of riparian areas along the Colorado Front Range: the effect of urbanization."

S. R. Morris, Canisius College, Buffalo, NY, "An introduction to taxonomy, classification, and cladistics."

M. Eagan, California State Univ., Chico, CA, "Design your own taxonomy."

E. H. Burtt, Jr., Ohio Wesleyan Univ., Delaware, OH, "Natural, sexual, and geographical variation among House Sparrows."

P. Houde, New Mexico State Univ., Las Cruces, NM, "Chickadee hybridization zones."

L. D. Igl, USGS, Biological Resources Division, Jamestown, ND, and B. M. Ballard, Texas A&M Univ., Kingsville, TX, "Habitat use of migrating and wintering grassland birds in southern Texas."

D. J. Prosser and R. P. Brooks, Pennsylvania State Cooperative Wetlands Center, University Park, PA, "Effects of beaver pond succession on avian community composition."

E. Stone, Univ. of Colorado, Boulder, CO, "Songbird associations among Gambel oak habitats in southwestern Colorado: towards a measure of biodiversity value."

R. E. Thill, USDA Forest Service, Nacogdoches, TX, P. A. Tappe, Univ. of Arkansas, Monticello, AR, M. A. Melchiors, Weyerhaeuser Company, Hot Springs, AR, and T. B. Wigley, Clemson Univ., Clemson, SC, "Breeding bird communities of streamside zones in the Ouachita Mountains, Arkansas."

A. T. Peterson, S. L. Egbert, and K. P. Price, Univ. of Kansas, Lawrence, KS, "When distributional models fail: mirroring ecology and history in geographic distribution."

K. T. Vierling, Univ. of Colorado, Boulder, CO, "Predation and source/sink population dynamics of Red-winged Blackbirds."

S. R. Dewey, Colorado State Univ., Fort Collins, CO, "Effects of food availability on parental care strategies and juvenile survival in Northern Goshawks."

D. A. Robinson, Jr., and E. J. Finck, Emporia State Univ., Emporia, KS, "Effects of food supplementation on nestling Eastern Bluebirds (*Sialia sialis*)."

D. L. Swanson and D. P. Weinacht, Univ. of South Dakota, Vermillion, SD, "Seasonal effects on metabolism and thermoregulation in Northern Bobwhite."

S. J. Cooper, Utah State Univ., Logan, UT, "Thermal and energetic consequences of roost-site selection in seasonally acclimatized Mountain Chickadees and Plain Titmice."

E. J. Willoughby, St. Mary's College of Maryland, St. Mary's City, MD, "Color change and molting in Lawrence's Goldfinch."

D. Klem, Jr., L. S. Crivelli, II, G. A. Davis, F. A. Lewis, III, and M. Elder, Muhlenberg College, Allentown, PA, "Bird-window collisions worldwide."

C. Dove, Smithsonian Institution, Washington, DC, "Forensic ornithology."

M. S. Funk, Roosevelt Univ., Chicago, IL, "Doing avian behavioral research at the zoo."

E. D. Kennedy and D. W. White, Albion College, Albion, MI, "A laboratory on form and function: feeding in birds."

S. K. Skagen, USGS, Fort Collins, CO, "Transitory populations in the Great Plains: the case of migrant shorebirds."

F. L. Knopf, USGS, Fort Collins, CO, "Ecology and conservation of the grassland 'shore-bird,' the Mountain Plover."

L. D. Martin, Univ. of Kansas, Lawrence, KS, "Ice Age biogeography of North American birds."

J. D. Rising, Univ. of Toronto, Toronto, ON, Canada, "Avian hybrid zones in the Great Plains."

J. Hughes, R. J. Robel, and K. E. Kemp, Kansas State Univ., Manhattan, KS, "Factors influencing avian productivity on Conservation Reserve Program fields in Kansas."

L. B. Best, Iowa State Univ., Ames, IA, H. Campa, III, S. R. Winterstein, Michigan State Univ., East Lansing, MI, K. E. Kemp, R. J. Robel, Kansas State Univ., Manhattan, KS, M. R. Ryan, Univ. of Missouri, Columbia, MO, J. A. Savidge, Univ. of Nebraska, Lincoln, NE, and H. P. Weeks, Jr., Purdue Univ., West Lafayette, IN, "Bird abundance and nesting in CRP fields and cropland throughout the Midwest."

P. T. Hughes, R. R. Moldenhauer, J. Graden, Sam Houston State Univ., Huntsville, TX, and R. Bunn, USDOD, Fort Carson, CO, "Abundance of shortgrass prairie birds on the Pinon Canyon Maneuver Site in southeastern Colorado."

D. H. Johnson, L. D. Igl, and M. D. Schwartz, Northern Prairie Science Center, Jamestown, ND, "Changes in breeding bird communities of CRP fields in the northern Great Plains."

R. R. Koford, Iowa State Univ., Ames, IA, "Fledging success of ground-nesting passerines in CRP fields in North Dakota and Minnesota."

T. D. McCoy, M. R. Ryan, E. W. Kurzejeski, and L. W. Burger, Jr., Univ. of Missouri and Missouri Dept. of Conservation, Columbia, MO, "CRP: source or sink habitat for grassland birds in Missouri."

POSTERS

M. E. Berry, Univ. of Colorado, Boulder, CO, "Habitat use by songbirds in northern Colorado Front Range foothills shrub: effects of vegetation structure and composition."

J. F. Chase, and A. Cruz, Univ. of Colorado, Boulder, CO, "Range of the Brown-headed Cowbird in Colorado—past and present."

C. Dove, Smithsonian Institution, Washington, DC, "Feather evidence helps clarify locality of anthropological artifacts in the Museum of Mankind."

H. Ewell and C. Bechtold, Univ. of Colorado, Boulder, CO, "An experimental corridor in Australia's rainforest."

S. W. Gillihan and M. F. Carter, Colorado Bird Observatory, Brighton, CO, "Bird populations in relation to level of western spruce budworm defoliation in a Colorado mixed-conifer forest."

H. T. Hendrickson, Univ. of North Carolina, Greensboro, NC, "Population trends of eastern House Finches (1946–1995)."

D. M. Juliano, B. J. Carner, J. C. Bednarz, and M. J. Huss, Arkansas State Univ., State University, AR, "Characteristics of nest sites used by Hairy Woodpeckers in western Washington."

T. J. Mabee, Colorado State Univ., Fort Collins, CO, "Using eggshell evidence to determine nest fate of shorebirds."

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J. A. Sedgwick, USGS Biological Resources Division, Fort Collins, CO, "Spatial and temporal variability in Brown-headed Cowbird parasitism of Willow Flycatchers."

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W. H. Busby, Kansas State Biological Survey, Lawrence, KS, and J. L. Zimmerman, Kansas State Univ., Manhattan, KS, "The Kansas Breeding-bird Atlas Project."

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Dr. Robert C. Beason will serve as Editor of *The Wilson Bulletin* beginning with Volume 110. All manuscripts submitted for publication in the *Bulletin* should be sent to him at this address:

Dr. Robert C. Beason
Biology Department
State University of New York
1 College Circle
Geneseo, NY 14454

email: beason@uno.cc.geneseo.edu
(or) wilsonbull@uno.cc.geneseo.edu

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